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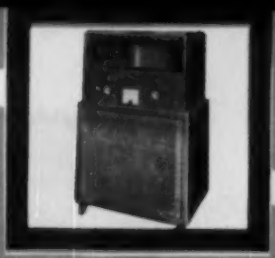

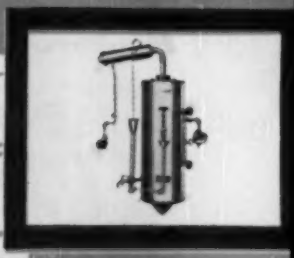

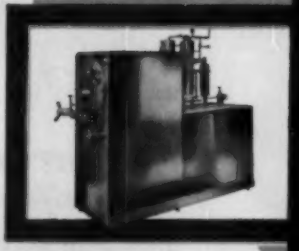

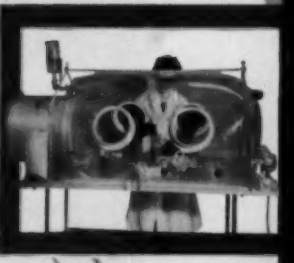

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THE QUARTERLY REVIEW of BIOLOGY

MECHANISMS OF CYTOKINESIS: A CRITICAL REVIEW

BY HENRY S. ROBERTS

Department of Zoology, Duke University, Durham, North Carolina

ABSTRACT

Current theories of cytokinesis are reviewed and critically analyzed. The expanding membrane theory and the theory of astral cleavage are shown to be unsatisfactory. Mechanisms which appear to have general validity are: (1) rounding up of cells as a result of the contraction of an actomysin-like substance in the cortex; (2) relaxation of polar cortex permitting continued equatorial contraction to cause furrowing; (3) new membrane formation. It is possible to describe cytokinesis in all cells, plant and animal, in terms of varying dominance of these factors in different cells.

INTRODUCTION

IN recent years a number of theories have been advanced which explain cytokinesis of animal cells on the basis of quite different mechanisms. When one compares the division of a fibroblast with cleavage of an amphibian egg, or cleavage of an echinoderm egg with cell-plate formation in plant cells, there is a strong temptation to conclude that different types of cells do employ fundamentally different mechanisms. Nevertheless, there are philosophical and theoretical considerations as well as observations which support the view that the same fundamental mechanisms may operate in all cells, variously modified by evolutionary events, physical structure, and environmental factors. Cell division undoubtedly existed prior to the evolutionary divergence which gave rise to the present variety of living forms and before cellular differentiation occurred in multicellular organisms. Conservatism characterizes biological change. It proceeds by modification and adaptation of the pre-existing, rarely by radical innovation. Karyokinetic mechanisms are strikingly similar in all living cells. It would be surprising if the subsequent division of the cytosome should be achieved by basically different mechanisms in different cell types. It would be even more surprising if amphibian fibroblasts and ova should divide by entirely different processes.

An exhaustive review of the literature is not intended. Current theories are critically analyzed with the goal of achieving the following: identification of those factors which appear to be common to all or most current theories and formation of some judgment of their validity; determination of whether on this basis it is possible by a process of synthesis to describe an overall mechanism capable of explaining the apparently contradictory evidences; and identification of problems on which further research is needed and whose solution would contribute materially to our understanding. The review is concerned primarily with cytokinesis of animal cells. There exist some evidences of similarity in dividing plant and animal cells. These are reviewed and summarized.

REVIEW OF THEORIES

Astral cleavage

K. Dan and coworkers devised a means of studying surface movements of cleaving eggs

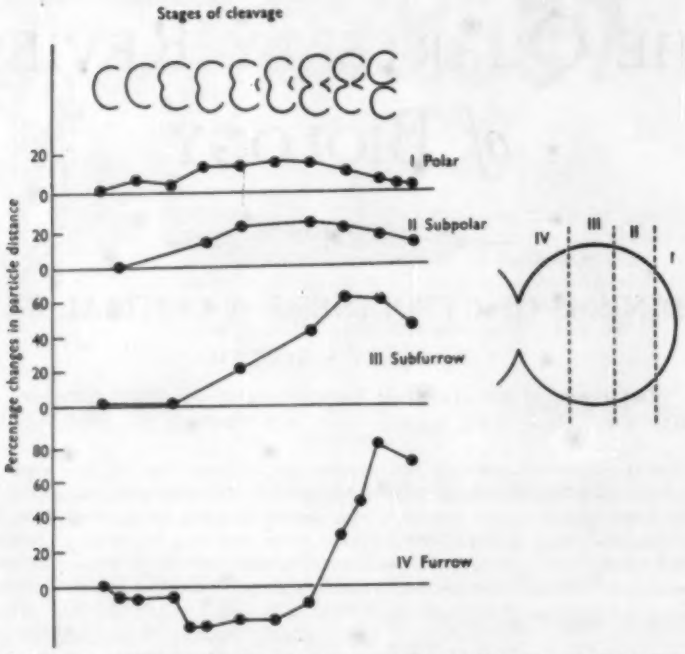

FIG. 1. PERCENTAGE CHANGES IN DISTANCE BETWEEN KAOLIN PARTICLES ON FOUR REGIONS OF THE EGG SURFACE. NAKED EGGS OF *Mespilia*
(From Swann and Mitchison, 1958, as adapted from Dan, Yanagita, and Sugiyama, 1937).

by measuring the linear movements of pairs of adherent kaolin particles with respect to each other and plotting the percentage change against the stage of cleavage. In a series of experiments on eggs of the echinoderms *Mespilia globulus* (K. Dan, Yanagita, and Sugiyama, 1937), and *Astriclypeus manni* (Dan, Dan, and Yanagita, 1938), and the snail, *Ilyanassa obsoleta* (Dan and Dan, 1942), a consistent pattern of surface movements was observed (Fig. 1). At the onset of cleavage a wave of expansion begins at the poles accompanied by a simultaneous contraction at the equator. Expansion begins progressively later in the subpolar and subfurrow regions and is of progressively greater magnitude. Initial shrinkage of the furrow region is followed by a relatively tremendous expansion in later cleavage. As the equatorial expansion begins, expansion ceases in the more polar regions and slightly later in the subfurrow region. Later there is a falling off from maximum values, leaving a residual expansion in interkinesis which is progressively greater from pole to equator. It was observed that presence of the hyaline layer tended to obscure these movements as though it were slipping over the true cell surface. The one exception to this pattern of surface movements is the furrow between the vegetal side of one blastomere and the attached polar lobe in *Ilyanassa*. In this furrow, which is not underlain by a spindle, only expansion occurs.

On the basis of these and other observations, K. Dan (1943, reviewed by J. C. Dan, 1948) proposed a detailed theory of astral cleavage which, in a sense, revived the earlier hypothesis of Heidenhain (1897) but added very extensively to the factual data underlying it and modified the interpretation. The astral centers are regarded as centers of gelation, developing rigid gelated spines. Apparently these spines are not entirely equivalent to astral rays since Dan states (K. Dan, 1943, p. 134), "In a large cell, in order for relatively long spines to exert a pull or push at their tips when the base is moving, some reinforcement to the spines may be necessary. The author thinks that the visible astral rays are highly specialized structures to accommodate such a necessity." The asters are thus spiny

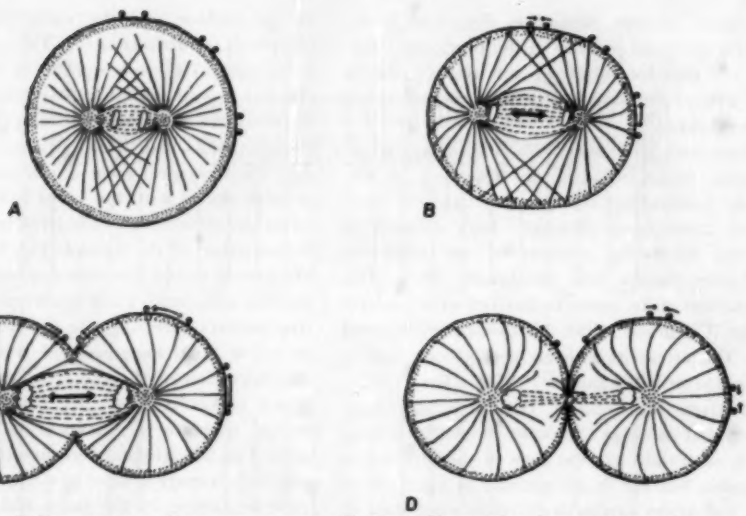

FIG. 2. DIAGRAMMATIC REPRESENTATION OF K. DAN'S THEORY OF ASTRAL CLEAVAGE
Adherent kaolin particles are shown by small circles on the surface and their movements by arrows.

spheres which grow at the expense of the more fluid endoplasm, reminiscent of Gray's theory of astral growth (Gray, 1924). K. Dan assumes that as the spines lengthen they become anchored in the gelated cortex and the spiny spheres intersect in the equatorial region, giving rise to the frequently described crossing of astral rays in this region (Fig. 2A, B). Astral growth also explains the commonly observed rounding-up of cells prior to cleavage.

Upon full development of the asters, active spindle elongation provides the driving force which results in subsequent events and ultimate cleavage. The rigid spines being pushed toward the polar regions are forced to bend outward in a "fountain" configuration. Since they are anchored in the cortex this results in a stretching or expansion of the polar surface. Simultaneously pulling toward their respective poles of the crossing spines in the equatorial region results in a shrinking of the equatorial surface (Fig. 2B). In this early stage the intermediate region of the surface is still unaffected. The growth of the asters and their movement into the more polar region result in a flow of fluid cytoplasm toward the equator, accounting for the subcortical endoplasmic currents described by earlier workers. Continued elongation of the spindle results in surface expansion spreading into the subpolar and subfurrow regions, while pulling of astral spines on the equatorial region causes the surface to be pulled in, giving rise to the furrow (Fig. 2C). Movement apart of the asters and endoplasm enclosed in the spaces between the spines creates a suction which sucks the furrow in. In later stages the spines are pulled away from the equatorial cortex and further advance of the furrow results from suction alone, causing now a stretching of the surface in the furrow region. Dan suggests that at this stage the bent polar spines "spring back" to some extent, accounting for shrinkage of the polar surface (Fig. 2D). In the terminal stages of cleavage new surface is formed around the connecting stalk between the two blastomeres.

In the original formulation of the theory it is at least suggested that anastral cells divide by the same mechanism: "it is possible to imagine that in cells of the anastral type, similarly formed gelation systems may be existing although they cannot be discerned morphologically" (K. Dan, 1943, p. 334). However, J. C. Dan in her review (1948, p. 192) states, "It is to be understood that this theory attempts to explain the division process only in cells whose cleavage is accompanied by the appearance of a typical mitotic figure. . . ." The theory has been extended to explain eccentric division (Dan and Dan, 1947a, b). More recently (K. Dan, 1954a, b), the theory has been revised by stating that

the "new" surface previously described is actually a stretched portion of the preexisting surface and that formation of new surface cannot be a part of the division mechanism but occurs in interkinesis.

Swann and Mitchison (1958) have summarized evidence which requires the rejection of any theory demanding the presence of an astral system throughout cleavage. Eggs succeed in cleaving following solation of the asters by colchicine (Swann and Mitchison, 1953), after destruction of the asters by stirring with a microneedle (Chambers, 1938; Mitchison, 1953b), and after the asters have been sucked out with a micropipette (Hiramoto, 1956). Fry (1925), Tharaldsen (1926), and Harvey (1940) have shown that cleavage can occur in enucleate fragments of certain marine eggs in the absence of a spindle, but not in the absence of asters. Spindles and asters undoubtedly play some part in cleavage, but they clearly do not function mechanically in the manner required by this theory. Apparently cells may cleave in the absence of either but not of both. The major, and invaluable, contribution of Dan and his coworkers is their analysis of surface movements during cleavage.

Expanding membrane theory

This theory and observations on which it is based were outlined in two papers by Swann (1952), and Mitchison (1952). Swann describes a wave of decreasing birefringence beginning in the equatorial region of the spindle and spreading poleward as the chromosomes move apart in anaphase, and moving outward over the asters when the chromosomes reach the poles. The asters are meanwhile growing. Cleavage begins when decrease in birefringence and astral growth are complete. Decrease in birefringence is attributed to a "structural agent" released by the chromosomes which induces a disorientation of protein structure of spindle and asters. The slow spread of decreasing birefringence is explained as the result of "trapped diffusion" in which molecules of the structural agent are bound by material in which they are diffusing. Swann argues strongly for nuclear (chromosomal) control of the entire mitotic cycle, including initiation of cleavage.

Mitchison defines the cell membrane as including both the thin lipid (permeability) layer at the surface and the underlying cortex or ectoplasm (structural layer). The cortex or structural layer of the sea urchin egg is described as about 1.5 μ in thickness (Mitchison, 1956). On the basis of birefringence studies (Mitchison and Swann, 1952; Mitchison, 1953b), he postulates that the structural layer is composed of looped protein chains with the loops radially arranged while the micellar axes are lying in all directions in the plane of the surface (Fig. 3). Such an arrangement would not only explain the observed positive tangential form birefringence and negative intrinsic birefringence but would also result in active areal expansion of the surface upon disorientation of the radial loops (Fig. 4). The figure makes it clear that such a membrane should decrease in thickness as it expands in area. The birefringence studies also show at the onset of cleavage a wave of decreasing birefringence beginning at the poles and spreading toward the equator. The decrease at the poles is accompanied by an initial slight increase at the equator. As the wave of decreasing birefringence reaches the furrow its birefringence falls also. Mitchison interprets this as evidence of a wave of disorientation of the structural layer and therefore expansion of the surface, precisely as described by Dan and coworkers. Mitchison states that Dan's experiments have been repeated, using the sea urchin, *Paracentrotus*, with substantially the same results.

According to the expanding membrane theory cleavage is initiated when the "structural agent" of Swann (X-substance of Mitchison) reaches the surface, inducing disorientation of radially looped proteins in the structural layer and consequently an active expansion of the surface. This is first observed at the poles because the chromosomes, the presumed source of the structural agent, are nearest the polar surfaces of the eggs. The wave of disorientation and consequent surface expansion spreads toward the equator as the structural agent reaches a more subpolar area (Fig. 5). In original formulation of the theory a slight elastic tension of the cell surface at the onset of cleavage was assumed. Consequently an elastic contraction of the equatorial region would occur simultaneously with the polar expansions, resulting first in a flattening of the equatorial region and then in the initiation of a furrow. By the time the expansion reaches the furrow all tension would be released, the furrow would have dipped inward far

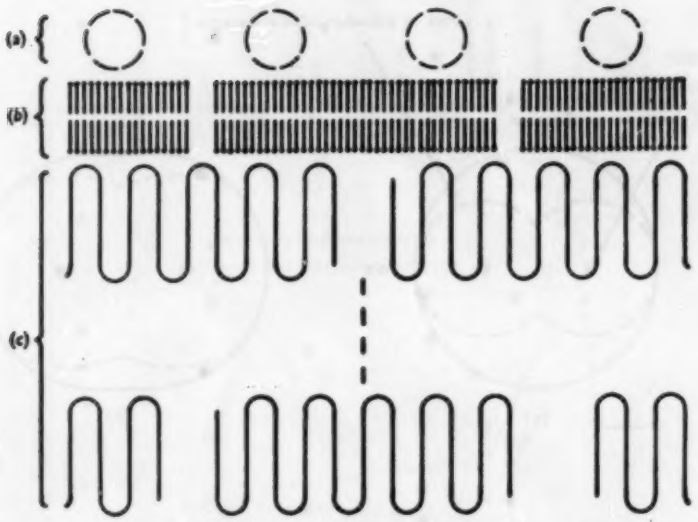

FIG. 3. MODEL OF MEMBRANE STRUCTURE.
(a) Layer of antigenic and antisphering protein. (b) 'Permeability' layer of lipids. (c) 'Structural' layer of protein. (From Mitchison, 1952).

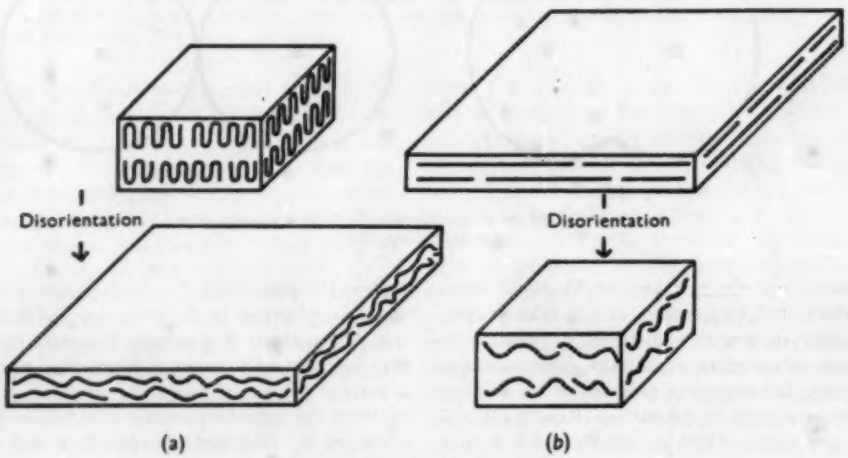

FIG. 4. MEMBRANE CHANGES
(a) Expansion in area of looped protein membrane. (b) Contraction in area of conventional protein membrane. (From Mitchison, 1952).

enough to be affected by the disorienting substance, and further advance of the furrow results from expansion of the furrow wall and push from adjacent regions. More recently the theory has been modified (Swann and Mitchison, 1958) on the basis of the finding of Dan and Ono (1954) that there is no areal expansion of the furrow wall during most of the time that the furrow is advancing. It is now assumed that the furrow wall is passive, becoming "plastic" and incapable of expansion as a result of the high concentration of structural agent to which it is exposed. Advance of the furrow is attributed entirely to push from adjacent regions.

Mitchison and Swann (1954a) have devised an ingenious cell elastimeter, for measuring

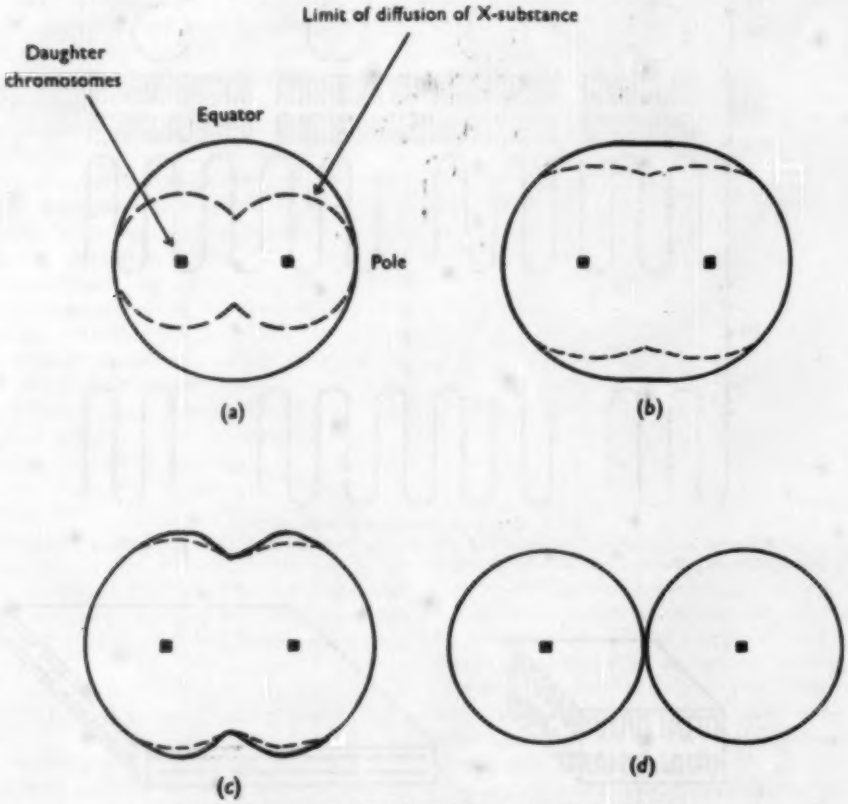

FIG. 5. DIAGRAM OF CELL DIVISION IN A SEA URCHIN EGG (From Mitchison, 1952).

"stiffness" of the cell surface. A small hemispherical bulge is sucked into a micropipette. Changes in negative hydrostatic pressure required to maintain a constant deformation of the egg surface give a measure of the stiffness or deformability of the surface. Results (Mitchison and Swann, 1955) are shown in Fig. 6. Stiffness begins to rise in metaphase, reaches a peak as cleavage begins, and declines during cleavage.

The theory encounters several difficulties, especially in its revised form. One requisite of the theory is that the internal pressure (and surface tension) must be zero if a "plastic" (deformable?) furrow is to be pushed through the interior of the cell. If surface tension is zero the furrow cannot be initiated by elastic contraction as originally postulated, and the question arises as to why the equatorial region turns inward instead of bulging outward. The authors suggest the possibility of a small initial tension which is exhausted in the early stages of furrowing. Alternatively they suggest that more energy may be required to bulge outward than to form a furrow! This still leaves the problem of explaining the initial equatorial contraction demonstrated by Dan and his coworkers and confirmed by Swann and Mitchison. These problems of internal pressure and surface tension have been investigated in a series of ingenious experiments which will be considered later in this review. Another requisite of the theory is that the membrane be sufficiently rigid to push upon itself as it expands to force the furrow inward. Expansion results from breaking bonds holding the proteins in radial loops, disorientation, and consequent thinning of the membrane. This is at the time maximum stiffness is required. The postulated membrane structure is

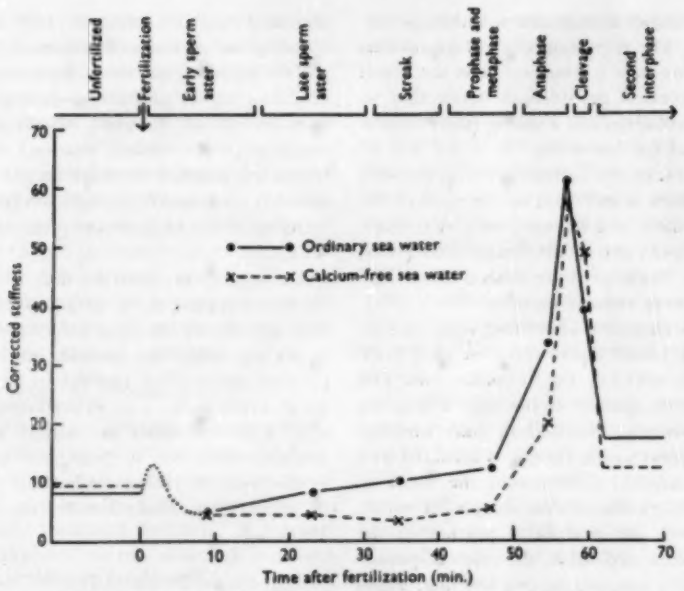

FIG. 6. STIFFNESS CHANGES DURING FIRST INTERPHASE AND DIVISION
Eggs of *Psammechinus miliaris*. Corrected stiffness in dynes/cm^2/μ deformation. (From Mitchison and Swann, 1955).

such that any disorientation must result in expansion, yet in considering the lack of areal expansion in the furrow it is stated (Swann and Mitchison, 1958, p. 128) "... we must make the quite reasonable asumption that high concentrations of this substance (structural agent) will so *disorient* the protein structure that it becomes plastic and *loses the power of expansion*."

Evaluation of the expanding membrane theory is dependent on analysis of the factors of internal pressure and surface tension. Consequently, it will be considered in a later section, Internal Pressure and Surface Tension, p. 167.

Cortical gel contraction

The concept of a contracting equatorial ring which constricts a cell into two is descriptive of what one sees in the division of a living cell. Consequently it has been invoked as a principal mechanism in cytokinesis by numerous workers, only two of whom will be discussed here. Lewis (1939, 1951) regarded protoplasmic gels as inherently contractile. Cleavage is described (Lewis, 1951, p. 1292) as "due to an increase in thickness and/or viscosity of a narrow equatorial part of the broad equatorial band of the gel layer. The increased contractile tension of the narrow constriction band constricts the cell in two." These two points, increased gelation (that Herbst had observed already in 1900) and contraction of the gelated protoplasm, are basic to theories of cortical contraction.

Marsland (1956a, b; Marsland and Landau, 1954) has proposed the most comprehensive and detailed theory of cortical contraction, based primarily on the effects of pressure and temperature on cleavage. Early cleavage stages of *Arbacia punctulata, Arbacia lixula, Echinarachnius parma, Rana pipiens,* and *Chaetopterus pergamentaceus* were subjected to fairly high pressures, 2,000–6,000 lb/in.^{2} at 20°C. At a critical pressure, characteristic of the species, furrows regressed. Furrowing resumed upon release of pressure. The critical pressure decreased at lower temperatures and increased at higher temperatures. Gel strength of the cortex of *Arbacia* eggs at different pressures and temperatures was determined by using as an index the time required to achieve a standard displacement of cortical granules at a uniform centrifugal force. Cortical gel strength decreased with increasing pressure and lowered temperatures and in-

creased with higher temperatures, within physiological limits. The regression of cleavage furrows under high pressure is interpreted as the result of reducing cortical gel strength below that required for furrowing, i.e., a strong (stiff) cortical gel is required for furrowing.

The behavior of the cortical gel with pressure and temperature is such that on the basis of the work of Marsland and Brown (1942), it is classified as a type II gel in the Freundlich (1937) classification. Such gels are endothermic and gelation involves volume *increase*.

Cleavage is visualized as starting with the contraction of a broad equatorial belt of gelated cortex which stretches the subpolar area and results in an elongation of the cell. The polar region is passively stretched or may undergo solation. As soon as the furrow is initiated as a result of equatorial contraction, the band of contractile cortex diminishes sharply in width, explaining why the peripheral portion of the furrow may show expansion, the result of passive stretching. It is assumed that in the final stages of furrowing (Marsland and Landau, 1954, p. 532) "the region of active contraction shifts from the trough of the furrow to the side-walls, first to the region immediately adjacent to the trough and later to a more peripheral site. . . ." It is also assumed that the gel at the very bottom of the trough, having reached maximum contraction, undergoes solation, preparing for approach and final fusion of the cell membranes. The gel immediately adjacent remains contracted, transmitting the force from more peripheral and still contracting furrow gel. A slight modification of this theory is suggested by Marsland in a later paper (1956b, p. 192) when he states, "Cytokinesis is initiated, apparently, by a localized solation which weakens the gel structure at each pole."

Marsland regards gelation as an essential prerequisite to contraction of an essentially fluid system such as protoplasm (Marsland, 1956b, p. 182). "Gelation represents the formation of a three-dimensional network from fibrillar units present in the system. Thus the contraction of a gel structure represents a rapid sort of syneresis, whereby the protein (fibrillar) components of the colloidal network undergo forcible folding, without relinquishing their intermolecular linkages." Landau, Zimmerman, and Marsland (1955) have demonstrated that gel strength of *Arbacia* and *Chaetopterus* eggs is significantly increased at all pressures and temperatures tested in the presence of adenosine triphosphate (ATP) added to sea water before cleavage. Significantly higher pressures were required to suppress furrowing. Landau, Marsland, and Zimmerman (1954) showed that gel strength and furrowing potency decrease in the presence of mersalyl acid, which strongly inhibits hydrolytic splitting of the high energy phosphate bonds of ATP.

These concepts and the data on which they are based appear to be valid and must be taken into account in any final solution. Major weaknesses are failure to consider initiation of the cleavage process and inadequate explanation of polar expansions. The experiments with ATP and ATP inhibitors are highly promising, a promise which has in great part been realized in the work of Hoffmann-Berling (1953; 1954a, b; 1956; 1960; Hoffmann-Berling and Weber, 1953).

Amoeboid movement

Although as outlined by Chalkley (1935, 1951) this theory would apply only to amoeboid cells, including fibroblasts and lymphocytes, it is of especial interest in that it provides a basis for comparing division of amoeboid cells and eggs, and suggests both cortical contraction and membrane expansion as significant factors.

Amoebae are observed to round up in prophase and to become quiescent except for minimal random pseudopodial activity. It is believed, on the basis of decreased activity of the contractile vacuoles, that internal pressure increases. Increased movement of cytoplasmic particles occurs when the nuclear membrane breaks down and adjacent to the anaphase chromosomes. This is interpreted as increased fluidity of the cytoplasm induced by nuclear components. When the daughter chromosome groups approach the cell surface the plasmagel layer "can be seen to solate." As a consequence of elastic tension the equatorial cortex contracts, the more fluid endoplasm is pressed into the weakened polar cortex, and polar pseudopodia are formed. Further and final separation of the daughter cells results from locomotion in opposite directions, stretching and breaking the connecting strand. When one daughter cell is prevented from attaching to the substrate it is absorbed by the attached cell, but not before a distinct narrow bridge has been formed be-

tween them by contraction of equatorial plasmagel. Endoplasm flows back and forth through the connecting stalk, correlated with pseudopod development and expansion.

Chalkley's theory, although antedating most theories here reviewed and although descriptive in basis, incorporates two of the three factors which appear to have fairly general validity, polar expansion and cortical contraction. In addition it postulates the initiation of equatorial contraction by differentiation of the polar cortex. Its essential points are incorporated in the astral relaxation theory, to be considered next, and in my more general hypothesis.

Astral relaxation

Wolpert (1960) has proposed a theory which although considerably more detailed and documented, greatly resembles the amoeboid movement theory of Chalkley (1935). Rounding-up of the cell and increased "stiffness" of the surface are interpreted as the result of increased tension of the cell membrane. Although (p. 180) "the sea urchin egg membrane is thus to be regarded as a thin-walled elastic membrane...", Wolpert apparently believes the increased tension to be more than elastic tension resulting from internal pressure, and states (p. 206), "It is thus very tempting to assume that the cell membrane has properties similar to muscle proteins or actomysin threads, but much more evidence is required to establish this view...." Furrowing is initiated by a decrease in tension at the poles, allowing the equatorial region to contract. Wolpert rejects the views of Chalkley (1935, 1951) and Swann (1952) that the chromosomes induce decreased tension, and expansion, of the polar surfaces. Since enucleate eggs have been shown to cleave he believes the asters, or a substance arising at the centrioles and associated with the asters, induce relaxation of the polar regions. The problem of anastral cells is not considered in detail, but it is suggested that in some apparently anastral cells astral fibers may actually be present. The contracting area of the furrow is believed to contract to nothing and the increased surface area required to result entirely from stretching of the existing membrane. Since he suggests that the membrane may be in some sort of equilibrium with the cytoplasm, it is inferred that new surface material may be added at any time by intussusception. It is stated that the theory is unable to account for the cleavage of the amphibian egg.

Cortical growth

A detailed study of the mechanism of cleavage in the egg of the newt, *Triturus alpestris*, was made by Selman and Waddington (1955). The study is particularly valuable in that it is concerned with an egg markedly different from the more usually studied echinoderm egg. The newt egg is larger (just over 2 mm vs. circa 100 μ), yolky, telolecithal, and has an eccentric spindle. The authors conclude that the principal mechanism is the formation of new cell surface, cortical growth.

Eggs and blastomeres round up during cleavage, becoming most nearly spherical at the moment the furrow appears, and subsequently relax. When small punctures are made only a slight slow outflow of yolk occurs, from which it is inferred that little internal pressure exists. Rounding-up is interpreted as the result of either an increase of Young's modulus or of an increased thickness of the elastic cortex. Movements of the egg surface were determined by following the movement of individual pigment granules and of pairs of granules with respect to each other. Areal changes were measured by planimetering prepared diagrams of pigment movement, using areas of approximately equal breadth and width outlined by as many granules as possible. The authors (Selman and Waddington, 1955, p. 728) state: "... cortical movements during cleavage in echinoderms are much greater, when recorded as percentages, than in the newt, yet they do not differ qualitatively except in the matter of timing," and (p. 711) "there is thus no evidence for any net change in the area of the pigmented surface during cleavage." Since it can easily be demonstrated that a net increase in surface is required in the division of an egg into two equal blastomeres, it appears that new surface must be produced. As the furrow deepens and opens up, white unpigmented cortex is revealed. In later cleavage the unpigmented cortex "retreats beneath the surface to form part of the cortex by which the daughter blastomeres remain in contact after cleavage." Patches of surface in the path of the advancing furrow were vitally stained with Nile blue. As the furrows crossed the stained areas they opened up to expose white unpigmented and unstained surface. The au-

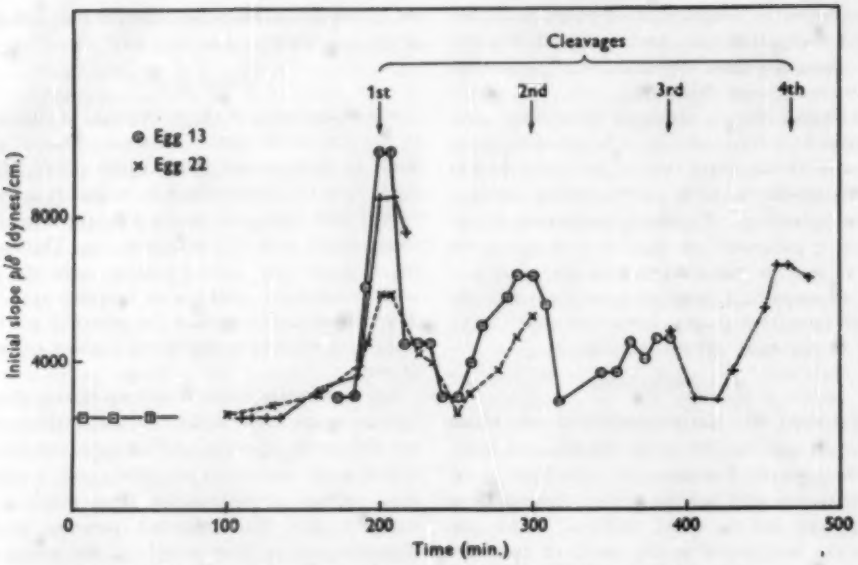

FIG. 7. VARIATION WITH TIME OF THE FLEXURAL RIGIDITY OF THE EGG SURFACE (From Selman and Waddington, 1955).

thors consider the possibility that white unpigmented cortex might result from expansion of a narrow band of surface to approximately ten times its original area, thus diluting the pigment so that it might appear white. This interpretation is rejected on the basis that the expanded area would be so thin "it could not possibly possess the mechanical rigidity demonstrated."

Rigidity ("resistance to flexure") of the cortex was measured by means of apparatus and methods similar to those used by Mitchison and Swann (1954a) in their elastimeter experiments, with broadly similar results. The results are summarized in Fig. 7, in which the ordinate p/δ is proportional to the flexural rigidity of the surface. The rigidity of the cortex varies in time, corresponding to observations on rounding-up of eggs, and reaches a maximum at the onset of cleavage and a minimum between cleavages. At comparable times all surfaces of the egg, including exposed unpigmented surface at the bottom of the furrow, gave "precisely similar" values. If, however, the micropipette was thrust deep into the furrow, pushing the blastomeres apart, values only half as great were recorded. It is suggested that in this region new surface is in the process of formation or that damage resulted from the procedure, since the surface stuck to the pipette and long strands of gel were pulled out as the pipette was withdrawn.

Serial sections of eggs fixed when the furrow appeared were examined by light microscopy. There were "clear signs of changes occurring in the subcortical cytoplasm in positions below and ahead of the furrow." Evidences included yolk displacement along a line in the plane of the furrow and local accumulations of small pigment granules along this line. At this time the cortical surface formed an unbroken line across the furrow surface and surface cortical pigment was not observed to move into the furrow. After light centrifugation the subcortical pigment was moved centrifugally, but the surface pigment and that along the modified cytoplasm were not moved, suggesting that the modified cytoplasm consists of a rigid gel. "In several instances, moreover, the pigmentation in the modified region formed two lines of granules at a separation of about 4 μ and this suggests that the new layer of gel may already be double."

On the basis of these observations a comprehensive theory of cleavage in the newt is proposed. Initially cortical rigidity is low so that the cell is flattened by gravity (Fig. 8A). Twenty to fifty minutes before first evidence of furrowing the cortex increases in rigidity, causing the

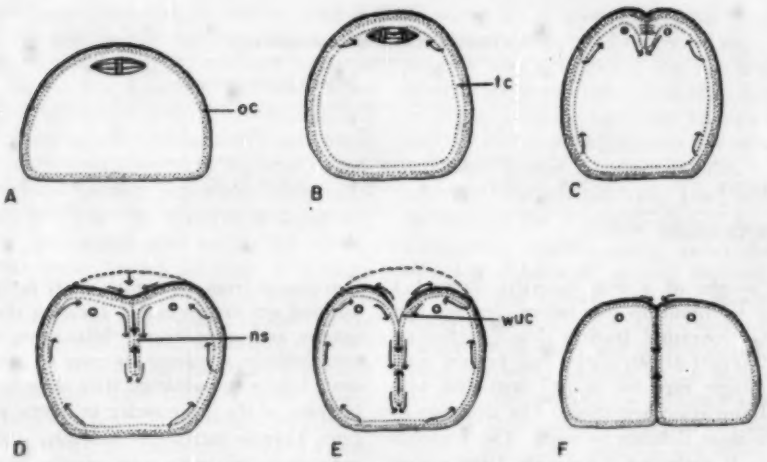

FIG. 8. DIAGRAMMATIC REPRESENTATION OF THE CORTICAL GROWTH THEORY
oc, original cortex; *tc*, thickened cortex; *ns*, new surface being formed; *wuc*, white unpigmented cortex exposed at bottom of furrow. Arrows indicate movement: in subcortical regions, of gelated cortex transported to area of new surface formation; in the furrow area, surface movements; in the new surface, contraction.

egg to round up (Fig. 8B). Increased rigidity is attributed to increased thickness of the cortex or possibly to an increase in Young's modulus. Cortical rigidity and rounding up reach a maximum at the beginning of cleavage. By late anaphase gelated material from the cortex is transported by cortical currents to the equatorial region of the spindle and accumulates to form a double layered new cortical gel extending toward the vegetal pole (Fig. 8B, C, D). Contraction of this gel sheet results in movement of surface pigment granules toward the furrow site and a "dipping-in" of the furrow region (Fig. 8D). The pigmented surface coat along the furrow parts, exposing the new unpigmented cortex (Fig. 8E). Continued growth extends the new cortex to the vegetal surface. Continuing contraction causes it to "retreat beneath the surface" so that it is restricted to the surface by which the blastomeres are in contact, and the pigmented animal surface is pulled again to the bottom of the furrow. The original cortex becomes less rigid as gelated material is removed into the newly forming cortex, and the blastomeres flatten under gravity (Fig. 8F). The area of original cortex is unchanged and all of the new surface required is provided by newly formed cortex.

Although as yet unconfirmed, these observations provide the first clear evidence that new membrane formation may be a significant factor in cytokinesis of animal cells. The resemblance to cell-plate formation in plants is apparent. The cortical growth theory thus offers the hope, and perhaps the basis, of arriving at a generalization encompassing the division of both plant and animal cells.

ANALYSIS OF MECHANISMS

Each of the preceding hypotheses involves certain phenomena associated with the process of cytokinesis. The following sections are devoted to analysis of these phenomena in an effort to form some judgment as to validity and applicability.

Rounding-up of cells

Rounding-up of animal cells before cleavage appears to be a general phenomenon. It is strikingly shown in dividing fibroblasts in tissue culture. Reference has been made to amoebae and the newt egg. Dividing epithelial cells seen in ordinary tissue sections are clearly rounded up in spite of their association with surrounding cells. Cohen and Berrill (1936) describe examples. Rounding-up in normally spherical cells such as echinoderm eggs would appear difficult to demonstrate. However, Danielli (1952) observed that sea urchin eggs slightly compressed

TABLE 1

*Size changes in developing starfish eggs**

	Minutes after Fertilization						
	Unfertil.	1′	2′	7′	10′	20′	70′
Egg diameter	3.4	3.4	3.4	3.4	3.5 × 3.55	3.5 × 3.6	3.5 × 3.6

* From Chambers, 1921.

by the weight of a thin coverslip showed a tendency to round up just before cleavage and raised the coverslip. During cleavage they relaxed. Wolpert (1960) states that he has compressed single eggs by 50 per cent and confirmed Danielli's observations. The situation in plants is more difficult to assess. The presence of rigid cell walls and, frequently, large watery vacuoles are complicating factors. Bajer and Mölè-Bajer (1956) have described the division of living endosperm cells of a number of higher plants. The cells were deliberately flattened prior to observation. "The lack of cellulose walls make possible the formation of cytoplasmic protuberances. These pseudopodia-like strings of cytoplasm may form during the whole division, but are most prominent in prophase and telophase. During pro- and metaphase the shape of the cell often changes to a sphere or an ellipsoid—often without pseudopodia formation. It is of interest that in other material the cells often become round before metaphase. In animal tissue it is well known that pseudopodia disappear before anaphase. . . . Endosperm cells often form outpushings during the telophase."

Rounding-up of cells correlates quite well with the curves of increasing "stiffness" determined by Mitchison and Swann (Fig. 6). It has a consistent relationship to the mitotic cycle: increasing during pro-, meta-, and anaphase, reaching a peak just prior to cleavage, and decreasing to a minimum during interphase. It is of considerable importance to cytokinetic mechanisms because of its relationship to internal pressure and membrane tension at the time of cleavage.

Volume increase is a possible explanation of rounding-up. Table 1 is from Chambers (1921). He states: "Not only does the egg not decrease in volume, but it slightly increases in size until segmentation occurs. The accompanying table is one sample of the measurements made. The conclusions from this table apply both to starfish and sea urchin eggs." Treating the eggs as spheres and using average diameters, these figures indicate a volume increase of over 13 per cent. I have unpublished data showing volume increase of the same order in beetle spermatocytes. Volume increase of this magnitude would indicate water uptake, since gelation of the whole cell would result in a volume increase of less than 1 per cent, based on the data of Freundlich (1937). Barber and Callan (1943) have inferred an uptake of liquid in the swelling of epidermal cells of the newt during anaphase and telophase. Jacquez and Biesele (1954) have calculated volume changes in a primary spermatocyte of *Psophus stridulus* from Michel's well-known film. The calculation assumes the cell to be an ellipsoid of revolution around the spindle axis. Their data show a high volume in prometaphase, a lower value in metaphase, a rise to maximum value in mid-anaphase, a minimum at the end of anaphase, and a slight rise until the beginning of cleavage in early telophase. There is no correlation with the described cycle of rounding-up or with changes in surface stiffness. However, their assumption that the cell measured was an ellipsoid of revolution is almost certainly incorrect. In Michel's preparations the cells lay between the coverslip and paraffin oil filling the well of a well slide. I have tried this type of preparation and found the cells to be significantly flattened, useless for volume calculations by this method. The marked clarity of internal structure in Michel's film is another evidence of significant flattening. Mitchison (1952, p. 117, footnote) says, "Preliminary measurements of the changes in cell volume during cleavage show that, if anything, the volume tends to diminish slightly." Swann and Mitchison (1958, p. 127) say, "Our measurements (unpublished) show, however, that there are no substantial changes in volume during cleavage."

Alternative explanations to volume increase involve changes in the surface. Selman and Waddington (1955) suggest increased thickness of the cortex, but increased thickness alone cannot cause rounding-up. Indeed, the cell might gel throughout without this result. Some increase in tension is required to cause rounding-up against gravity. Mitchison (1956) and Hiramoto (1957) find no evidence of significant change in cortical thickness. Swann and Mitchison (1958) argue for an increase in Young's modulus, an alternative admitted by Selman and Waddington, on the basis of their elastimeter experiments. However, as will be seen in the next section, their results can be equally as well explained in other ways. Wolpert (1960, p. 177) has discussed at length "gel strength" of the cortex as measured by Marsland and Landau (1954) and concludes, "There can be little doubt that 'gel strength' is not a measure of those properties which determine the ease with which the membrane can be deformed and thus determine the shape of the cell. 'Gel strength' is a property of the cortex, but its significance is quite unclear." It should be recalled that Marsland and Landau regard cortical gelation as a *prerequisite* for contraction. As such, it does have a relationship to contractile forces which might determine the shape of the cell and mechanical properties of the surface. There is now convincing evidence that rounding-up does result from contraction of an actomysin-like substance in the cortex. It will be discussed in detail later in this paper.

Internal pressure and surface tension

The presence or absence of internal pressure and surface tension is crucial to the expanding membrane theory. If either is present furrowing cannot occur by the postulated mechanism, although the authors argue that the existence of a small internal pressure may be irrelevant. Both are either essential to or expected from the theories of cortical contraction, amoeboid movement, and astral relaxation. Neither is critical for the cortical growth theory.

Most of the evidence against internal pressure and surface tension comes from the ingenious experiments of Mitchison and Swann (1954a, b; 1955). Reference has already been made to their elastimeter experiments (p. 159). They admit that for any given stiffness value there is a series of solutions for Young's modulus and internal pressure varying from no internal pressure and a relatively high modulus to a high internal pressure and a relatively low modulus. In an effort to arrive at a solution of the problem and to obtain absolute values of Young's modulus they resorted to model experiments using rubber balls with known Young's modulus, wall thickness, and internal pressure. They state: "The justification for such a procedure comes from dimensional analysis, which shows that if the ratios of cell diameter, cell-wall thickness, pipette diameter and deformation are preserved, the negative pressure in the pipette and the positive pressure in the ball will vary linearly with the elastic (Young's) modulus of the ball. In other words, if the model is a precise scaling-up of the elastimeter, and the suction required for a given degree of deformation is n times as great as with the elastimeter, then the internal pressure of the ball and the modulus will both be n times as great as in the cell." The model experiments were scaled up 1,000 times. There are a number of stated and implied assumptions. The first is that the cell is a thick-walled elastic sphere, "like a tennis ball, which by virtue of its thick wall has a certain rigidity and does not collapse even when the tension in its wall is released by puncturing it." Wolpert (1960) discusses this assumption and concludes that it is not valid. It is also assumed that the membrane resembles rubber in having the same Poisson's ratio and the same relative values for the different moduli. This assumption is certainly questionable. The authors describe the viscous behavior or "creep" of the cell surface, which "is presumably due primarily to true viscous flow within the cell surface." Selman and Waddington (1955, p. 120) have pointed out that this assumes that the cell surface is isotropic like rubber, "which is unlikely if the structures involved here are at all similar to those described by Mitchison (1952). It is, moreover, probable that the inner wall of the gel cortical layer has no definite boundary." Such an assumption also neglects the dynamic "fluid" nature of the cell membrane cited by Wolpert (1960, p. 176). In order to get a seal between the pipettes and the rubber balls, the surfaces of the rubber balls were greased. The assumption must be made that the slipping over the edge of the pipettes was the same for the cell surface and the greased rubber surface.

Results based on assumptions such as these

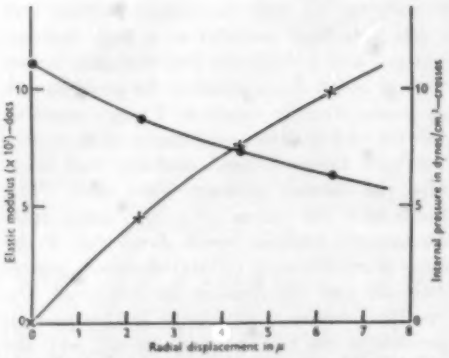

FIG. 9. YOUNG'S MODULUS AND INTERNAL PRESSURE FOR A 100 μ EGG
(From Mitchison and Swann, 1954).

are certainly doubtful. Of particular importance is Fig. 9 (Mitchison and Swann, 1954a; Text-fig. 16) because of its use in this and subsequent experiments on swollen and shrunken eggs. The text makes it clear that it is a restatement of information presented in a previous graph and based entirely on the rubber ball experiments. The data are used to set an upper limit for internal pressure of 95 dynes/cm² for unfertilized eggs. The validity of this figure is measured by the validity of the assumptions on which the model experiments are based.

In their experiments on swollen and shrunken eggs (Mitchison and Swann, 1954b, 1955), unfertilized eggs, eggs in the sperm aster stage, and late anaphase and cleavage stages were subjected to media of varying tonicity and their "stiffness" determined with the elastimeter. Only the late anaphase and cleavage stages will be considered here since we are concerned only with whether internal pressure and surface tension are present at cleavage. However, comments on methods, interpretations, and conclusions are equally applicable to the other stages. Table 2 summarizes the results. The media used are appended to the table for convenience. The half and full hypertonic media were not used with these eggs *because they inhibited cleavage*. They state (Mitchison and Swann, 1955, p. 740), "A test ($P = 0.05$) shows that, although the difference between the stiffness in full hypotonic and in normal sea water is significant, the other differences are not." It seems clear that these eggs in full hypotonic sea water cleaved, since they state, "owing, however, to the rapid changes in stiffness that take place at this stage (cleavage), there was a wide scatter in the measurements . . .", and the more hypertonic media were not used because they inhibited cleavage. In other words cleavage occurred under conditions of significant internal pressure and membrane tension. It could hardly be argued that increased stiffness in the full hypotonic medium is due to an increase in Young's modulus since (p. 744) to explain anomalous results with sperm aster eggs it is suggested that in hypotonic medium the membrane becomes hydrated and therefore weaker. In the wrinkling experiments hypertonic sea water (50 ml sea water + 15 ml 2 M NaCl) was used on late anaphase eggs. Wrinkling of the surface was first observed at this concentration after a 9 per cent shrinkage in diameter. Wrinkling would indicate zero membrane tension. Since cleavage is inhibited in media of this tonicity, one can only wonder if this is because of the absence of tension. Using these data, the calculated Young's modulus, and the data in Fig. 7, the authors calculate the maximum possible pressure to be 500 dynes/cm². Again this figure is only as valid as the assumptions in the model rubber ball experiments. If the hypertonic medium in these wrinkling experiments changed the properties of the membrane by dehydrating it, another possible source of error exists. The writer can only agree with Wolpert (1960, p. 188), who concludes, "These results cannot be regarded as evidence against an increase in tension, and, if anything, they tend to support it."

There are other evidences as to the existence of internal pressure and surface tension, and the ability of cells to cleave when both are present. The microdissection experiment of Chambers (1938, 1951) in which one blastomere of a sea urchin egg cleaving in isotonic KCl solution was sliced open and the other blastomere shrank, discharging its contents through the furrow region, appears to be evidence for membrane tension. But Mitchison (1953b) was unsuccessful in repeating this experiment, using eggs of different species, so it must be regarded as inconclusive. However, Danielli (1952), Wolpert (1960), and Scott, (1946, 1960a) describe experiments in which cleavage was successful in markedly compressed eggs where membrane tension and internal pressure almost certainly were present. Chambers (1938, 1951) showed that a sea urchin egg would still cleave if stretched by microneedles so that the membrane was certainly

TABLE 2

*Stiffness of swollen and shrunken eggs, Psammechinus microtuberculatus**

Stage	Medium	Molarity	No. of eggs	Average diameter (μ)	Corrected stiffness (dynes/cm²/μ deflexion for 100 μ egg and 30 μ pipette	
					Mean	Standard deviation
Late anaphase and early cleavage	Full hypotonic	0.39	37	119	56.0	29.9
	Half hypotonic	0.45	19	115	36.5	22.5
	Normal	0.54	15	110	34.4	16.6
	Quarter hypertonic	0.67	18	105	45.9	19.8
		Composition of Medium				
	Full hypotonic	50 ml Ca-free sea water + 20 ml dist. water				
	Half hypotonic	50 ml Ca-free sea water + 10 ml dist. water				
	Normal	Ca-free sea water				
	Quarter hypertonic	50 ml Ca-free sea water + 5 ml 2M NaCl				

* Adapted from Mitchison and Swann, 1955. Composition of medium added from text.

under tension. Chalkley (1935, 1951), and Scott (1946) have observed flow of endoplasm through the furrow stalk while cleavage is progressing, a clear indication of pressure. Fig. 10 is a previously unpublished record by the author of a cell division in which the furrow steadily advanced while the incipient daughter cells alternately expanded and contracted with flow of cytoplasm back and forth through the stalk. Division was successfully completed. A chromosomal bridge, indicated by the heavy line, was apparent during the first ten minutes. Dashed lines delimit the chromosomes. This is clear evidence of successful cleavage under conditions of undoubted membrane tension and internal pressure.

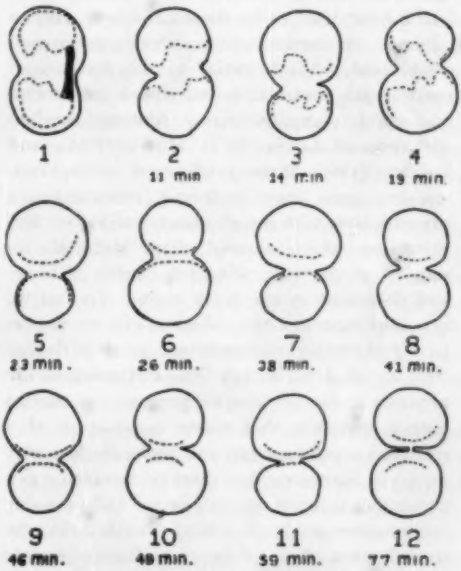

FIG. 10. SUCCESSFUL CLEAVAGE UNDER CONDITIONS OF UNDOUBTED TENSION AND INTERNAL PRESSURE

Tracings from a time-lapse film record of division of an irradiated undifferentiated embryonic cell of *Chortophaga viridifasciata*.

According to the expanding membrane theory cleavage cannot occur if membrane tension and internal pressure are present, other than a minimal amount which would be exhausted in the early stages of membrane expansion. On the basis of available evidence the author must agree with Wolpert (1960) that this theory must be rejected.

Polar expansions and cortical contraction

Few factors in cleavage seem as well established and generally accepted as expansion of the polar surfaces. The adherent kaolin particle experiments of Dan, substantiated by Mitchison, and evidence from the birefringence studies of Swann and Mitchison show conclusively that this is a consistent factor in sea urchin cleavage. Waddington states that cortical movements in the newt egg differ only in degree and timing. Chalkley has described solation of the polar cor-

tex and the formation of polar pseudopodia in amoebae. Chambers (1951) and Lewis (1951) have described polar blebbing in dividing fibroblasts in tissue culture. The polar blebs of hemipteran spermatocytes shown by Bowen (1920) are well known. I have shown (Roberts, 1955) that in dividing grasshopper neuroblasts clearly visible waves of polar expansions occur sequentially, first at that pole which will give rise to the larger daughter neuroblast and later at the ganglion cell pole. There seems to be no evidence concerning polar expansions in plant cells other than the already quoted statement of the Bajers (p. 166) concerning "cytoplasmic protuberances," and their statement leaves it unclear whether there is any preferential association with polar regions.

The astral cleavage mechanism of K. Dan and the expanding membrane theory of Swann and Mitchison have been rejected in the previous discussion. Except for the factor of new membrane formation, to be considered later, furrow advance by cortical contraction appears well established. It is essential to the theories of cortical gel contraction, amoeboid movement, and astral relaxation already discussed, and to the views of Lewis (1951), Huber (1946), and Lehman (1946). Direct evidence of cortical contraction stems from Wolpert's (1960) constant pressure runs with the elastimeter of Swann and Mitchison which showed that "stiffness" increased in the furrow region during cleavage and decreased in the polar region. To this we may add Scott's (1960b) observations on the behavior of cortical echinochrome granules during cleavage of *Arbacia* eggs. The discussion in the previous section on internal pressure and surface tension indicates that elastic contraction of a stretched membrane can and probably does play a part in furrowing, but there is convincing evidence that it is not the only factor and probably not a major one. Scott (1960a) described the continued contraction of tubes of furrow surface isolated from the remaining cortex by cuts. His figures show a degree of contraction impossible to explain on the basis of simple elastic contraction. Reference has been made to the demonstration by Marsland and his coworkers that ATP has a marked effect on furrowing.

The most exciting and most promising experimental evidence is that of Hoffman-Berling (1953; 1954a, b; 1956; 1960; Hoffmann-Berling and Weber, 1953). The 1960 paper is an especially valuable summary. Muscle cells, amoebae, fibroblasts, epithelial cells, ascites tumor cells, and other living cells in interphase and during division were extracted by glycerine solutions in the cold for various periods of time, producing dead "models" of cells with relatively intact structure but with the cell membrane destroyed. This is presumably the plasma membrane or lipid "permeability" membrane of Mitchison. If this is the case, the experiments to be reported were done on cells with a naked cortex. He states that there is "good reason to suppose it is not cell membrane but cytoplasmic structures which are the motor of cytokinesis." His accompanying reference to the work of Marsland seems to make it clear that by "cytoplasmic structures" he means the cell cortex. Crystalloids, metabolites, and a large part of the globular proteins are said to be extracted. Similar models can also be prepared in aqueous solutions containing cytolytic substances such as saponin. Such models retain "motile" structures and their vital arrangement is maintained. The following observations on such cell models are reported:

(1) An actomysin-like substance has been extracted from sarcoma cells which, although it contracts 100 to 1,000 times more slowly than muscle actomysin, splits ATP and has the essential properties of actomysin.

(2) Fibroblasts contain a relaxing factor (Marsh-Bendall factor) similar to that of muscle cells. In briefly extracted models appreciable amounts of relaxing factor are still present but it is completely removed by long extraction. The relaxing factor has the following properties:
   (a) It prevents ATP splitting at physiological (and higher) ATP concentrations but does not prevent splitting at low ATP concentrations.
   (b) Large amounts of Mg^{++} are required.
   (c) Relaxing factor activity is suppressed by 10^{-6} M Ca^{++}.

(3) Completely extracted interphase models contract in physiological concentrations of ATP but briefly extracted models do not, unless Ca^{++} is added. Briefly extracted models will contract in low concentrations of ATP. It appears that ATP splitting is essential to contraction and that the relaxing factor is evenly distributed in interphase cells.

(4) Briefly extracted anaphase models cleave

in physiological concentrations of ATP but completely extracted models contract all over and round up. This is interpreted as meaning that the relaxing factor is in high concentration in polar regions and in low concentration in the furrow region. Thus ATP splitting is facilitated in the furrow region, permitting contraction and cleavage. Cleavage is not complete, the daughter "cells" being connected by a significant stalk. At physiological ATP concentrations spindle elongation and anaphase chromosome movements occur. Under conditions which inhibit spindle elongation chromosomes have occasionally been observed to move apart.

(5) It is suggested that "living interphase cells contain so much ATP that contraction does not occur unless ATP-resynthesis is reduced."

(6) Fibroblast models which have rounded up under the influence of ATP return to the extended form if treated with ATP concentrations high enough to prevent splitting. It is suggested that ATP binding rather than splitting is involved, and the same or a different protein may be responsible. It is noteworthy that all measures which inhibit constriction promote elongation (return to the extended form).

There could hardly be a more convincing demonstration that furrowing is a process of active contraction and that polar expansion is essential to furrow development. However, certain alternatives present themselves. It seems possible that the differential behavior of poles and furrow area could be explained on the basis of different concentrations of Ca^{++} rather than of relaxing factor. If, as a consequence of karyokinetic phenomena, Ca^{++} were in lower concentration in the polar cortex and higher in the furrow region the same effects would be expected. On the basis of Mazia's (1959) finding that the isolated mitotic apparatus strongly binds calcium, Wolpert (1960) suggests that the asters might remove calcium from the polar region so that the relaxing factor is no longer inhibited there. It would seem feasible to design experiments using Ca^{45} to test this alternative. It also seems possible that "elongation" of contracted interphase fibroblasts may be no more than a return to original form upon inhibition of contraction and that no special mechanism is involved. Elongation of cleaving fibroblast models is an expected consequence of equatorial constriction and polar expansion. Some caution in extrapolating directly to the living cell is needed. Hoffmann-Berling cautions that the procedure is not without artefact, in particular gelation of endoplasm. The relaxed condition of living interphase cells may be the consequence of calcium distribution rather than excess ATP. Conditions of turgor and elastic tension are not likely to be the same in living cells as in models with their plasma membrane removed, but the evidence does suggest that turgor and elastic tension, whatever part they play, are not essential to cleavage. New membrane formation cannot be evaluated in a model whose membrane has been destroyed and from which crystalloids, metabolites, and a large part of the globular proteins have been extracted.

Initiation of cleavage

From the work of Hoffmann-Berling it is apparent that the problem of initiation of cleavage is essentially that of the differentiation of the polar cortex or the furrow region, or both. If cleavage is to occur, relaxation of the polar cortex or facilitation of contraction of the furrow region, or both, must occur. There can be no doubt that the mitotic figure or some portion of it is responsible for bringing this about. Conklin (1917), Harvey (1935), Clement (1935), Carlson (1952), Waddington (1952), and others have shown that shifting the position of the mitotic figure affects the location of the furrow, and I have shown (Roberts, 1955) that experimentally altering the size of the spindle and its association with the cell surface also shifts the furrow position. There is convincing evidence that whatever the mechanism may be, it is in operation by the beginning of anaphase but not earlier than late metaphase. The most direct evidence is that of Hiramoto (1956), who demonstrated that the mitotic figure can be removed from the sea urchin egg during anaphase and occasionally in metaphase without altering the site of the furrow. The mitotic figure has been destroyed by colchicine (Beams and Evans, 1940; Swann and Mitchison, 1953), and podophyllin (Cornman and Cornman, 1951) prior to furrow formation, yet cleavage occurred. The mechanism continues to operate during anaphase and cleavage. Harvey (1935) showed that when the mitotic figure was shifted by centrifugation a

furrow, usually abortive, always appeared in the expected original position and a new furrow was formed in relation to the new position of the mitotic apparatus. Certain of the microdissection experiments of Carlson (1952, Fig. 9) show a similar effect as evidenced by visible membrane expansion.

There is convincing evidence that asters alone, in the absence of chromosomes or spindle, can initiate cleavage. Harvey (1936, 1940) has demonstrated that "red halves" of *Arbacia* eggs which lack a nucleus can be activated parthenogenetically and develop to the blastula stage. A monaster first appears, divides into two, and a furrow develops between the two asters. There is no spindle. Lorch (1952) has also described the appearance of cleavage furrows between the asters and enucleate eggs. See also the review of Briggs and King (1959). Wolpert's astral relaxation theory postulates that it is the asters which differentiate the polar cortex, causing it to relax. He suggests that apparently anastral cells may nevertheless have astral rays. Carlson (1952), in the apparently anastral grasshopper neuroblast, encountered resistance to movement of the microneedle between spindle pole and cortex, suggesting the presence of invisible astral rays. Östergren, Koopmans, and Reitalu (1953) describe asters in *Allium* root tip mitoses observed by phase microscopy. Östergren (1954) lists 16 genera and 17 species of higher plants in which he finds asters or astral rays at mitosis. There are, however, anastral cells in which the presence of astral rays is extremely unlikely. In spermatocytes of the llaveiine coccids described by Hughes-Schrader (1948), the spindle appears to be formed entirely of chromosomal fibers. Each chromosome forms its own spindle unit independently and only later do these units become associated in a bipolar configuration, which in some species has broadly dispersed poles and divergent fibers. It is difficult to argue against an assumption that astral rays must be present even though not demonstrated. Nevertheless, the anastral condition is so common that it does not appear justifiable to attribute cortical differentiation entirely to asters.

Swann (1952) and Mitchison (1952) have attributed the initiation of polar expansions to the chromosomes. Swann's observation of a wave of decreased birefringence which is attributed to diffusion of a structural agent released by the chromosomes has already been described (p. 158). Chalkley (1935, 1951) also believes that the chromosomes initiate cleavage by inducing a solation of the polar cortex. There appears to be little direct evidence in support of this view. Fankhauser (1934), and Harvey (1940) have shown that egg cells with reduced chromosome number cleave much more slowly than those with the diploid number. Other evidences of this sort are found in the review of Briggs and King (1959). In any event the control center for differentiation of the polar cortex appears to be the polar region of the spindle, whether amphiastral, anastral, or purely chromosomal. Evidence as to how the differentiation is achieved and what part nuclear (chromosomal) factors may play does not seem to be available. I have suggested (Roberts, 1955) that the interaction of centromeres and spindle poles with fibers of the achromatic figure during the period of anaphase chromosome movements may be a factor. This period should include metaphase also.

New membrane formation

It can be demonstrated that as a consequence of cell division the cell surface must be increased by roughly 30 per cent, more if a sphere divides into two equal hemispheres and a little less if it divides into two equal spheres. Cell plate formation in plant cells and cortical growth in the newt egg demonstrate that increase of surface by new membrane formation may be the principal mechanism in cytokinesis of some cells. It remains to be determined whether new membrane formation is a basic and important mechanism in the division of all or most animal cells. Certainly the cell surface cannot be stretched indefinitely by repeated division. New surface must be provided at some stage. There is no doubt that interphase cells can form new surface. Many cells if punctured or slightly torn will, if the medium is suitable, form a new surface on the cytoplasm which flows out. This suggests that necessary new surface could be formed as a post-cleavage event, but provides no evidence that this is actually what occurs. It is necessary to keep in mind the distinction between the plasma membrane ("permeability" layer of Mitchison), probably corresponding to the layer approximately 100 Å thick seen with the electron microscope, and the considerably thicker cortex or "structural" layer. The prob-

lem of new formation of the two layers may not be the same.

Wolpert (1960) argues on geometric grounds that increased surface is provided entirely by stretching during cleavage. Presumably new membrane is formed as a post-cleavage event. In his original formulation of the astral cleavage theory, K. Dan postulated that new membrane is formed around the connecting stalk in the terminal stages of cleavage. In later papers (K. Dan, 1954a, b), he argues that the apparent new membrane is a consequence of stretching and that new membrane is actually formed in interkinesis. The observations on which this interpretation is based merit detailed analysis because of the possibility of arriving at exactly opposite conclusions. In *Hemicentrotus* and *Arbacia* eggs, pigment granules in the cortex provide an excellent index to cortical contractions and expansions. In very late cleavage, according to K. Dan, into early interkinesis, pigment granules are concentrated around the connecting stalk, indicating contraction. "Shortly after cleavage" the accumulation around the connecting stalk disperses so that pigment temporarily becomes uniformly distributed, but continues so that "in the next moment" color due to pigment fades on the furrow side. Simultaneously the furrow surfaces of the blastomeres bulge toward each other and pigment becomes more concentrated in the polar area, indicating contraction. During the latter half of interkinesis pigment distribution again becomes uniform, and this is a prerequisite for the next division. According to K. Dan, the disappearance of pigmentation around the connecting stalk and in the furrow surface is simply the consequence of stretching of the existing surface. Contraction of the polar cortex and the pull of "attachment fibers" extending from the hyaline layer to the furrow surface is indicated as the cause of stretching. New surface is believed to be formed in late interkinesis when pigmentation again becomes uniform.

It is surprising that the most contracted portion of the surface, that around the connecting stalk, should suddenly at the end of cleavage not only relax but be stretched so thin that it bulges out and pigmentation disappears. Exactly the same result would be expected if new, easily deformable cortex formed at the base of the furrow were stretched by the elastic tension of the original cortex when active equatorial contraction ceased. It should be recalled that Selman and Waddington (1955) found the new cortex of the newt egg to be sticky and only half as resistant to deformation as the original cortex. The Cornmans (1951) have pointed out that a critical stage exists at the terminal stage of furrowing. "When the furrow is nearly completed, a process separate from those which caused the furrow to advance is required to complete the separation of the blastomeres." Johnson and I (Roberts and Johnson, 1956) found a similar critical stage just at the end of cleavage of multi-spindle beetle spermatocytes. In Hoffmann-Berling's (1960) fibroblast models, in which new membrane could not be expected to be formed, cleavage was not completed but ceased when a relatively stout stalk still remained. Motomura (1935, 1941), working also with *Hemicentrotus* (*Strongylocentrotus*) and *Temnopleurus*, believes that new surface is formed at the cleavage plane in urchin eggs.

There is little evidence as to the source of new membrane, whenever it may be formed. Selman and Waddington (1955) suggest that gelated cortex might be transported by cortical currents to the cleavage plane and build up new surface, but there is no actual evidence. Motomura (1950) has described the accumulation of basophilic cytoplasmic vacuoles in the cleavage plane of *Temnopleurus* eggs and of argyrophilic vacuoles in the cleavage plane of *Hemicentrotus* (*Strongylocentrolus*) eggs. He believes that these vacuoles "supply some substance taking part in the formation of the new cell surface. . . ." The most direct evidence comes from Porter and Machado's (1960) electron microscope studies of dividing onion root tip cells. New membrane formation here is by fairly typical cell-plate formation. In permanganate-fixed material, but apparent also in lead-stained osmic-acid-fixed material, the new membrane is seen to be formed by the fusion of tubular elements, derived from a fraying of the cisternae of the endoplasmic reticulum. The membrane thus formed appears to be the plasma membrane. Mercer and Wolpert (1958) have described the participation of apparently similar tubular elements in the formation of a "new layer" or membrane at or near the surface of cleaving sea urchin eggs. Mercer and Wolpert do not identify the tubular components as endoplasmic reticulum or derived from it, but they are strikingly similar to those shown by Porter and Machado. The new layer or membrane is not identified but

it is suggested that it may be mechanically involved in cleavage. It is probably not "new membrane" formed in the cleavage process, since it is already present in early cleavage and extends over the entire egg surface. It seems possible, though not suggested by the authors, that it may represent the establishment of new surface following the elevation of the fertilization membrane.

Such limited evidence suggests that the source of new plasma membrane may be cytoplasmic vacuolar components or endoplasmic reticulum. Much more evidence is required.

Furrowing in plant cells

In attempting to consider how cytokinesis in plant and animal cells might be related, the difficulty is encountered that most descriptive accounts of cytokinesis in plants date back thirty years or more, and experimental work is scarce. More recent work is concerned principally with details of cell-plate and cell-wall formation. According to Sharp (1934, pp. 109–110, 165–168), furrowing is not uncommon. He describes it as occuring in myxomycetes, certain algae and fungi, and in pollen mother cells of a number of angiosperms. Farr (1918) lists other examples. *Spirogyra* (McAllister, 1931), *Tetraspora* (McAllister, 1913), and possibly *Eremosphaera* (Mainx, 1927), which earlier were thought to divide by furrowing, have been shown to employ cell-plate formation. It is possible that poor fixation has led to other errors. However, Farr (1918) has observed division by furrowing in living *Magnolia* pollen mother cells. In this material a cell plate appears after the first nuclear division but the cell fails to divide. The cell plate disappears and, after the second nuclear division, furrows divide the cell into four microspores. It appears that in plant cells cytokinesis by new membrane formation is the rule, but furrowing does occur; in animal cells furrowing is the rule, but division by new membrane formation also occurs.

SUMMARY

Certain factors emerge from the preceeding reviews and analyses which appear to be reasonably well established, are capable of explaining the observations reported, and which can result in cleavage.

(1) Cells round up prior to division as a consequence of the contraction of an actomysin-like substance in the gelated cortex. ATP is split to provide energy for contraction. Volume increase may occur but, on present evidence, does not seem to be essential. Cortical contraction results in internal pressure and the observed increase in cortical stiffness prior to cleavage.

(2) Furrowing is initiated by relaxation of polar cortex resulting from either an increased concentration of relaxing (Marsh-Bendall) factor in the polar regions or by removal of calcium from polar regions. Alternatively, but less likely, equatorial contraction might be facilitated by decreased relaxing factor or increased calcium in the equatorial cortex. Asters alone, in the absence of spindle and chromosomes, are able to bring about cortical differentiation. In anastral cells containing spindles composed entirely of chromosomal fibers originating from the centromeres, the spindle poles appear to be the centers of cortical differentiation. Whatever the mechanism may be, it is in operation by the end of metaphase and continues to be effective until toward the end of furrowing. It is suggested that the interaction of centrosomes or centromeres, or both, with fibers of the achromatic figure may be a factor.

(3) New membrane formation is a factor of varying significance, difficult to assess. In the newt egg and in plant cells dividing by cell-plate formation it appears to be the predominant factor. In cells which employ furrowing it seems probable that new membrane formation may take place in the stalk at the base of the furrow and is a final necessary stage for the completion of cytokinesis. It is possible that in some or all cells dividing by furrowing new surface is formed during interkinesis. The evidence is inconclusive. The limited evidence available suggests that cytoplasmic vacuolar components, probably tubular elements derived from endoplasmic reticulum, fuse to form new plasma membrane.

On this basis it is possible to describe cytokinesis in all cells, plant and animal. In relatively small animal cells with cell centers and lacking impeding accumulations of yolk or other materials, furrowing by equatorial contrac-

tion plays the dominant role. New membrane formation makes a small but perhaps essential contribution to the process, or may be delayed until interkinesis. In large yolky cells such as the newt egg cortical contraction and furrowing initiate the division process but new membrane formation assumes a major role. In most plant cells the presence of rigid cell walls, the absence of cell centers, and possibly the absence of a well-developed gelated cortex, result in the virtual suppression of cortical contraction. Here new membrane (cell-plate) formation is the principal, perhaps the only, effective factor. In those plant cells, however, where physical (and chemical?) factors such as the absence of cell walls and, possibly, the presence of a differentiated cortex permit, furrowing may play a major and perhaps the principal role. In the foregoing discussion I have proposed a comprehensive hypothesis capable of describing cytokinesis in all cells, plant and animal. It is satisfying in terms of the philosophical and theoretical considerations mentioned in the Introduction, but much more evidence is required before it has a firm basis. The role of new membrane formation in animal cells such as the sea urchin egg, and for that matter confirmation of new membrane formation in the newt and similar eggs, require much more study. The factors of rounding-up and cortical contraction in plant cells are almost unknown, and especially here further research and information are needed.

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SOME PROBLEMS OF REGENERATION

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ABSTRACT

This review discusses the origin of the regeneration blastema, and particularly the importance of the skin, the skeleton, and other tissues in the process of regeneration. Also considered are reactions of regenerates to irradiation, including the effect of partial irradiation and the regression of regenerates. Especial attention is given to regeneration under abnormal conditions and to abnormal regeneration. The final section is concerned with the problem of stimulation of regeneration and the possibilities of regeneration in mammals.

INTRODUCTION

THE purpose of the present review is to survey the most important papers concerning some problems of regeneration. In most cases, attention will be given only to new papers which have not been discussed by previous reviewers. In some cases, however, certain data from much older papers will be considered in connection with new investigation. Purposely the scope of the present review was limited so as to make no mention of old literature. The reader can find adequate discussions of older papers in earlier general reviews of the regeneration problem (Korschelt, 1927; Nicholas, 1955).

Also, some special problems of regeneration will not be touched upon in the present review, because they are well described in certain extensive and comparatively new special reviews, e.g., "Regeneration of the Lens in the Amphibian Eye" (Reyer, 1954), "Regeneration of the Retina, Iris, and Lens" (Stone, 1959), and "The Influence of the Nerve on Regeneration" (Singer, 1952, 1959). The principal subject matter of this review is regeneration in amphibia; but in the last section, consideration is given also to regeneration in mammals.

The capacity for regeneration is a residue of the original capacities for growth, organization, and differentiation (Weiss, 1939). In some forms, regenerative power is enormous, whereas in others it is almost absent. Generally speaking, the percentage of good regenerators is lower among the higher forms than among the lower, more simply organized forms. Nevertheless, some lower forms (e.g., the ctenophores and the rotifers) have no regenerative capacity; and, on the other hand, some incomparably higher forms (e.g., the crustaceans and the amphibians) have extensive ability to regenerate. Moreover, closely related forms such as earthworms and leeches may have very great differences in regenerative capacity (Weiss, 1939).

ANALYSIS OF THE REGENERATION PROCESS

An excellent quantitative histological analysis of regeneration in *Triturus viridescens* has been made by Chalkley (1954, 1959). In this species, a clot is rapidly formed over the surface exposed by amputation, and the adjacent epithelium begins to migrate over the wound within 15 to 45 minutes. This migration, which appears to be complete within 24 hours or less, is not associated with local epidermal cell division. A similar mesenchymal migration occurs beneath the wound surface as dissociated cells, emerging from the stump tissues, accumulate between the wound epithelium and sub-epithelial tissues. The mesenchymal immigration continues for at least 72 hours. During this time, there is dedifferentiation of old tissues of the stump adjoining the exposed surface. The intercellular substance of bone and cartilage becomes dissolved, the connective tissue fibers likewise disintegrate, the muscles also undergo dedifferentiation, and the myofibrils disappear. The cells of all tissues become similar in appearance to embryonic cells (Balinsky, 1960).

Litwiller (1939) amputated the right anterior

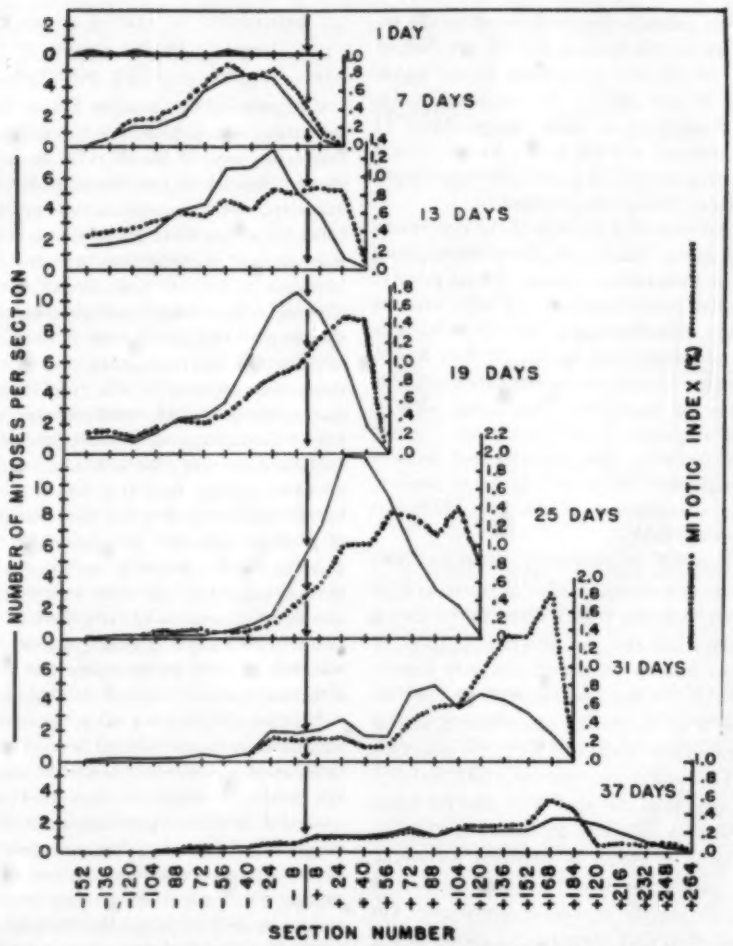

FIG. 1. CHANGES IN MITOTIC INDEX AND MITOSIS DISTRIBUTION IN BLASTEMA AND CONNECTIVE TISSUE ALONG THE AXIS OF THE REGENERATING LIMB
The index (dotted lines) is expressed as per cent of cells per section. No data are given for the first day. Arrows indicate the amputation plane. (Chalkley, 1954.)

limb of the Japanese newt, *Triturus pyrrhogaster*, at the base of the limb. He reported an accumulation of 9,000 cells during the first 15 days, in the complete absence of mitosis. Bassina (1940) observed in *Triton taeniatus* an accumulation of 15,000 cells, without mitosis, in less than 6 days.

According to Chalkley (1954, 1959), the mitotically active zone in *Triturus viridescens* migrates in a distal direction from stump to regenerate, and there is a shift in the distribution of cells. By the seventh day, there is a clear increase in the number of cells, but all in the proximal portion of the limb. On the thirteenth day, the distal nature of the accumulation is distinct; but at this time the mitotic index in the proximal parts of the limb is at its highest (Fig. 1). Beginning with the thirteenth day, the region of maximal cell accumulation begins to move distally.

The rapid growth of the distal accumulation and the migratory movements begin before the seventh day. At that time, the regenerate is the site of only 2 per cent of the observed mitoses, but contains 17 per cent of the newly formed cells. Simultaneously with this, the region of

peak mitotic index is also transferred to the regenerate. By the nineteenth day, 23 per cent of the newly added cells are present in the regenerate, but 29 per cent of the mitoses are distributed through these same tissues. After 37 days, the average mitotic index has decreased markedly. In processes like these, the importance of cell migration is to be emphasized.

The major source of the cells of the regenerate is the old stump. There are three overlapping stages in the formation of the regenerate proper: (1) an initial distal migration of cells without cell division, contributing a few thousand cells at most and terminating within the first 3 or 4 days; (2) migration of mitotically produced cells from stump to regenerate, beginning some 4 days after amputation and producing a minimum of 60,000 cells; and (3) continued division of these migratory cells in the regenerate proper, producing a minimum of 100,000 additional cells (Chalkley, 1959).

Production of regeneration blastema cells begins in the old stump. A mass of blastema cells occupies not only the region distal to the amputation plane, but also the proximal portion of the stump, instead of dissociated soft tissues. Only in 25 days is the mitotic activity of the regenerating limb so clearly concentrated that it can be reasonably identified with the blastema (Fig. 1). This is also the time at which redifferentiation begins in the regenerate and the number of blastema cells rapidly decreases (Fig. 1). During the early stages of blastema accumulation, it is possible to identify a large number of mitoses with specific tissues at the stump. On the seventh day after amputation, about 68 per cent of all mitoses can be identified with stump tissues, whereas the remaining 32 per cent of the cell divisions are those of the blastema. During the next 18 days, mitosis can be observed only in blastema cells. On the thirty-first day, many mitoses can be observed in new differentiated tissues. On the thirty-seventh day, only 30 per cent of the mitoses can be considered as blastema cell division (Chalkley, 1959).

Weiss (1939) has proposed the hypothesis that the blastema is a mass of equivalent cells which later differentiate in different ways. According to Lecamp (1947), cultivation of blastema cells in vitro produces cultures that are indistinguishable from connective tissue cultures obtained from non-regenerating parts of the organism.

IMPORTANCE OF SKIN IN REGENERATION; PROBLEM OF THE ORIGIN OF THE REGENERATION BLASTEMA

Godlewski (1928) was the first to describe the migration of epidermal cells and their transformation into blastema cells. Rose (1948) reviewed Godlewski's original observation, and expressed the opinion that the epidermis might furnish a major share of the young blastema during normal regeneration, assuming that the blastema is derived from dedifferentiating epidermal cells. Many authors, however, have shown that this conclusion is incorrect. Rose's hypothesis was based on the demonstration of a compensatory loss of cells from the epidermis during the period of rapid increase in the number of blastema cells in the regenerate. This occurs between the sixteenth and twentieth days. Chalkley (1954), however, found that the only epidermal losses observed in a limited number of animals occurred between the seventh and thirteenth days, and did not extend to the epidermal cap. Since the data were obtained from sacrificed tissues, these irregularities can be attributed to sampling errors, particularly as the number of cells in the epidermis is subject to irregular changes through molting or growth.

Manner (1953) observed accumulation of epidermal cells in the wound area. These cells remain in the epidermis, however, and never enter into the blastema proper. Heath (1953) observed that the epidermis graft did not participate in the formation of the blastema. Brunst (1944) observed complete failure of the regeneration blastema to form after heavy X-ray irradiation, in spite of the fact that the epithelium of the irradiated region shows normal mitotic figures.

Finally, Hay and Fishman (1960), working with limb tissues of *Triturus viridescens* labeled with tritiated thymidine, have recently reported direct evidence that apical epidermal cap cells do not contribute to the regeneration blastema of this animal.

According to Weiss (1950), "That the epidermis exerts some essential influence in the regeneration process has been known.... That some of its cells may escape into the blastema is quite credible; but from this to the assertion that they actually take part in the formation of the deeper limb tissues is a rather broad jump. Since this assertion is based solely on unconvincing observations and crude calculations,

without crucial experimental support, it can hardly stand up in the face of overwhelming experimental evidence to the contrary."

Nevertheless, it has been established that skinless stumps cannot regenerate. Polezhayev and Faworina (1935) showed that the regeneration anlage does not grow in the absence of epithelium, and that regeneration is suppressed by replacing the epithelium of the head. It is clear that the skin may play an essential role in manifesting the regenerative ability of the mesodermal portion of the amphibian limb.

Similar results were obtained by Morosow (1938). He transplanted the regenerates of axolotl extremities without skin epithelium under the tail skin. The regeneration process was completely suppressed. When the transplanted regenerates had epithelium, however, the regeneration process continued and produced atypical limbs.

Goss (1957a) made a special investigation of this problem, extirpating half of the limb in order to study regeneration from the remaining parts. Two variations of this technique were used (Fig. 2). From the right limb of newts, the posterior half was excised. This involved the removal of bone and muscle, but the skin was left intact. In the left limbs of the same animals, similar operations were performed except that the posterior half of the skin was removed along with the underlying mesodermal tissues. After amputation, the resulting regenerates from the right and left limbs were analyzed comparatively. On the right side, normal regeneration occurred, forming a complete regenerate. On the left side, only half of the distal extremity regenerated. Goss concluded that the regulatory capacity of the regenerating half limb is dependent upon the presence of a full complement of skin on the stump. The skin, therefore, is regarded as playing an essential role in the mechanisms of regeneration. Because of technical limitations, it has not been possible to determine which component of the skin, dermis or epidermis, is involved in mediating the regulation of mesodermal defects during regeneration.

According to Weiss (1939), tissue culture shows that differentiation of cellular character in a vertebrate is irreversible. This means that once a definite course of differentiation is established, a cell will never again be able to switch into another course. Therefore only dedifferentiation of structure is possible, but no change in the character of the cell. Only modulations are reversible. It is possible that a large proportion of the blastema originates from indifferent elements which have been mobilized from the unspecialized cells in the connective tissues of the stump (reserve cells). Cells from destroyed muscle and skeleton also have taken part in blastema formation. Nevertheless, since it is impossible to say whether or not they ever contribute to any structures other than muscle and skeleton, their participation in the blastema neither proves nor disproves the irreversibility of differentiation (Weiss, 1939).

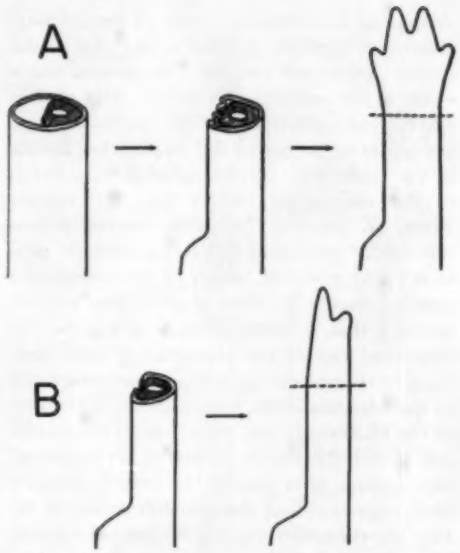

FIG. 2. DIAGRAM INDICATING TECHNIQUE AND RESULTS
A. Posterior half of the limb is removed, but the skin is left intact; after amputation, a complete regenerate is formed. B. Posterior half of the limb, including the skin, is removed; only one-half of the distal extremity is regenerated. (Goss, 1957.)

According to Thornton (1942), muscle tissue may in part dedifferentiate into blastema cells. The factors which determine the pattern of development in the blastema have a field character; the blastema forms the limb as a whole. The differentiation of a limb regenerate is directed and controlled by the limb field of the stump. The body as a whole has no influence upon the character and orientation of a regenerate. The limb growing from a salamander blastema implanted in a frog is a salamander limb; frogs' limbs are not able to regenerate (Weiss, 1939).

In a new investigation with larvae of *Amblystoma* (*A. tigrinum*, *A. opacum*, and *A. punctatum*), Thornton (1960) observed shifting of the

established epidermal cap from its normal position to an eccentric position at the edge of the healed amputation surface. This shifting was a result of the removal of a narrow strip of skin (dermis and epidermis) parallel and adjacent to the posterior border of the amputation surface of the limb. The movements of the epidermis of the amputation surface over this narrow wound in the skin during the healing process carried the epidermal cap to its eccentric position at the posterior border of the amputation surface. Results of these experiments support the view that, in larval *Ambystoma* at least, the epidermal cap of the regenerating limb functions to control the aggregation and outgrowth of the blastemal cells. Obviously the asymmetry of the blastema is not a result of an asymmetrically directed histolytic activity of the epidermal cap, because it is possible to induce complete limb regression and tissue dedifferentiation before the epidermal cap has become established. The regressed limb remnant is composed of mesenchyme cells derived from dedifferentiation of the limb tissues. The aggregation of these mesenchyme cells beneath the eccentric cap therefore must be due to a directing influence by the cap on their accumulation and outgrowth rather than to any kind of histolytic action by the epidermal cap. The exact nature of this influence of the epidermal cap on the blastemal cells of the regenerating limb is unknown, however.

Regeneration involves a differentiation of parts that occurs definitely de novo within an originally homogeneous and equipotential mass of cells (regeneration blastema) (Weiss, 1939).

IMPORTANCE OF THE SKELETON AND OTHER TISSUES IN THE REGENERATION PROCESS

The skeleton is the first tissue that differentiates in the regeneration blastema. Various investigations have been made concerning the regeneration of boneless limbs. Bischler (1923), Weiss (1925a), Brunst (1932), and others have shown that normal regeneration occurs even when the femur is removed from the hind limb and amputation is done through the boneless region. The regenerates contain cartilaginous skeleton formed distal to the level of amputation.

According to Weiss (1925a, 1939), the "limb field" directs the normal morphogenesis of the blastema even when some portions or tissues are missing, because the limb regenerates as a whole.

The "limb field" or "regeneration field" of Weiss (1925a, 1926) is identical with the "regeneration territory" of Guyénot and Ponse (1930). The regeneration territory is responsible for regeneration of a definite portion of the body; e.g., the tail. So long as a small piece of the tail remains, regeneration is possible. If, however, the tail is completely removed to the level of the last sacral vertebra, the whole "tail territory" is removed, and regeneration does not occur. Only wound healing is observed (Balinsky, 1960).

To study the role played by the limb in the future development of the blastema, many investigators have replaced the skeletal element normally present in the limb by other elements from another region of the same extremity. In most cases, the regenerates were more characteristic of the foreign skeletal element (Liosner, 1939; Umanski, 1939; and others). Okada (1936) obtained definitely tail-like regenerates from limbs containing tail vertebrae. Weiss (1925a), however, obtained normal regeneration from limbs in which the humerus and the femur were exchanged.

It is significant that most of the instances of bone substitution resulting in alterations of the regenerates involved replacement of a bone of the normal limb with one from another level of the same or another limb, whereas replacement with a bone from the corresponding segment of another extremity tended to have little or no effect on the subsequent regenerate. This phenomenon therefore appears to be due to differences between the limb levels involved, rather than between types of appendages (Goss, 1956a).

Critical interpretation of these data, however, necessitates consideration of the fact that the transplanted bones may well have been accompanied by adventitial connective tissue and even muscle, which might also have affected the differentiation of the blastema (Goss, 1956a). The developing blastema is capable of compensation for a deficiency in the stump from which it is formed, but it cannot accommodate for other types of alterations in the stump if they involve replacement of its components.

According to Goss (1956a), implantation of extra bones into the limb, with subsequent amputation through the treated region, is followed by the production of corresponding super-

numerary skeletal elements in the regenerate (Fig. 3). The paradoxical observation that the blastema is able not only to regenerate skeletal elements not present in the stump, but also to form extra ones corresponding to supernumerary subjacent bones, can be explained on the basis of two complementary hypotheses. The former phenomenon reflects the effect of the limb field, which enables the blastema to compensate for a deficiency of certain skeletal elements on the stump; the latter process is explained by a tissue-specific induction of individual cartilaginous elements formed by periosteal cells from corresponding skeletal structures on the stump.

The same effect can be obtained by addition of the lateral mandible or the ceratobranchial element of the first branchial arch to the limb, and by addition of limb or mandibular bones to the tail; obviously there is no specificity concerning the relation between the bone and its site of transplantation. It has been mentioned that the "limb field" (Weiss, 1925a, 1939) is the over-all organization of the blastema, but it should also be noted that individual limb tissues are capable of inducing specific histodifferentiation in the overlying blastema. According to Goss (1956a), these two mechanisms, mutually reinforcing in character, are to be regarded as an instance of "double assurance." Thus the blastema can accommodate for deficiencies in the limb stump, such as might be expected to occur rather frequently in nature as a result of injuries; but there is no adaptive provision for preventing the regeneration of supernumerary compounds, the chance occurrence of which is extremely rare.

The addition of glass rods, muscle, or devitalized bones does not induce supernumerary skeletal formation in the regenerate. Irradiation of transplanted bones inhibits skeletal regeneration. The mechanism by which accessory bones are regenerated is believed to involve the accumulation of osteoblasts in the immediately adjacent blastema, where their major role is to induce chondrification of the surrounding cells (Goss, 1956a).

Experiments were done in which forelimbs of adult *Triturus* were grafted together for the purpose of learning whether the regenerate produced after amputation of such double limbs would be single or double (Goss, 1956b). First a longitudinal incision was made in the ventral skin of both arms from the elbow to the wrist.

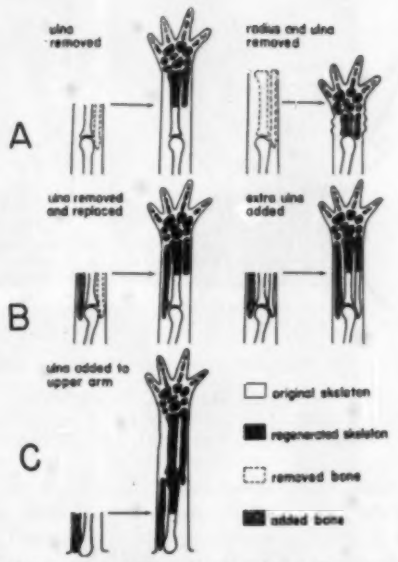

FIG. 3. SCHEMATIC RECAPITULATION OF RESULTS OF EXPERIMENTS INVOLVING REMOVAL OR ADDITION OF SKELETAL ELEMENTS IN SUBSEQUENTLY REGENERATED FORELIMBS
(Goss, 1956)

Then, using a needle and thread, a loop was directed beneath the skin, but around the radius and ulna of the two limbs (Fig. 4), and tied securely along the outer surface. Duplicated lower or upper arms were capable of regenerating single extremities, but in many cases the regenerates were either partially or completely double (Fig. 5, A–E). This shows that there is a high degree of regulation between the two regenerating components, giving rise to bilaterally symmetrical structures (Goss, 1956b).

In order to investigate the replacement of skeletal elements in the amphibia, bones were removed from the extremities of anuran tadpoles and larval and adult urodeles (Goss, 1956a). From these experiments, it was concluded that skeletal regenerations occur only if the extirpated structures are cartilaginous and if they are removed from a limb otherwise capable of regeneration after amputation. Probably, skeletal regeneration depends upon the developmental state of surrounding tissues: i.e., after skeletal extirpation in larval or recently regenerated urodele limbs, sufficient potential chondroblasts persist to ensure replacement; but chondrogenic cells in adult limbs, being restricted to the periosteum, are nearly all removed with the bone.

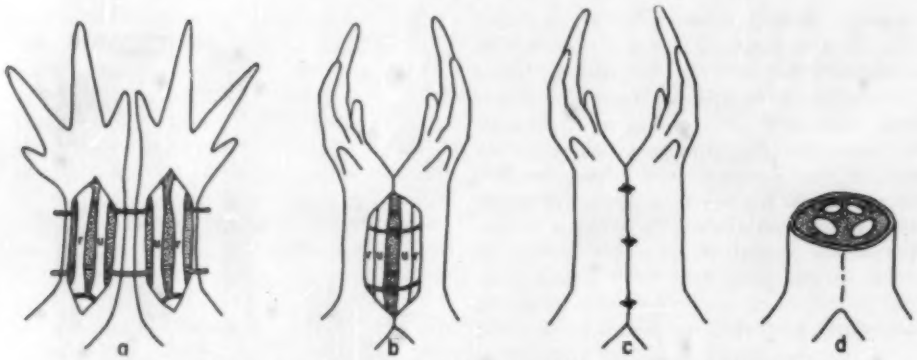

FIG. 4. DIAGRAMS ILLUSTRATING MAJOR STEPS IN OPERATIVE TECHNIQUE EMPLOYED IN GRAFTING LOWER LIMBS TOGETHER

Threads are directed around the radii and ulnae, but beneath the skin (a), tied as the ventral surfaces of the limbs are joined (b), and the skin is sutured (c). After healing for two weeks, the compound limb is amputated (d). (Goss, 1956b.)

Glade (1957) showed that normal regeneration of the *Triturus* limb can be altered if the end of the stump receives grafts of tail skin and spinal cord at the time of amputation. The resulting formations are usually chimeras, with both hand and tail characteristics, or sometimes almost complete heterotopic tails. Histological study of the limbs showed that the development of limb structures was inhibited in most of the cases, and that tail structures had formed instead, e.g., tail fin, segmental muscle, and cadiform skeletons.

The muscles may be important for determining the course of regeneration. When the muscles of the tail are replaced with muscles transplanted from a limb, the transplanted muscles influence the process of regeneration, and the regenerate has a structure resembling a limb (Liosner and Woronzowa, 1936). According to Holtzer (1959), the degenerating muscle fibers are the major source of mesenchymal blastema cells.

Examination of blastema cells with the electron microscope (Hay, 1958) showed that the cytoplasm of the early blastema cells is characterized by numerous free ribonucleoprotein granules and a discontinuous vesicular endoplasmic reticulum. The cells have abundant cytoplasm and are in close contact. After a period of rapid cell division, the morphology of the blastema cell changes. Cytoplasm is now sparse and contains a high concentration of free ribonucleoprotein granules, but little endoplasmic reticulum.

The cells of a very young regeneration blastema are completely undifferentiated and are able to develop in various ways. Such a young blastema may be transplanted to the amputation stump of a different organ, and then may develop in accordance with its new position. An early forelimb blastema transplanted to the stump of an amputated hindlimb is capable of developing into a hindlimb (Balinsky, 1960). The regeneration blastema of the tail has been transplanted to the shoulder region, and developed into a forelimb (Weiss, 1927).

EFFECT OF PARTIAL IRRADIATION ON MORPHOGENESIS OF LIMB REGENERATES

Irradiation with X-rays is an important tool for investigating regeneration (Brunst, 1950a). Two new investigations of the regeneration process by means of X-ray irradiation are considered in this section. Lomovskaya (1948) investigated the regeneration of the axolotl limb after irradiation of tibial or fibular halves with 7000 roentgens (r). To protect half of the limb from radiation, she inserted a lead plate between the tibia and fibula, and bent this plate around the tibial or fibular portion of the limb. She observed normal regeneration from partially irradiated limbs.

Goss (1957b) irradiated the hind limbs of adult *Triturus viridescens* with 2000 r. Either the anterior (tibial) or posterior (fibular) halves of such limbs were irradiated, the remaining parts being shielded with small rectangular pieces of lead 2 mm thick (Fig. 6, A). After ir-

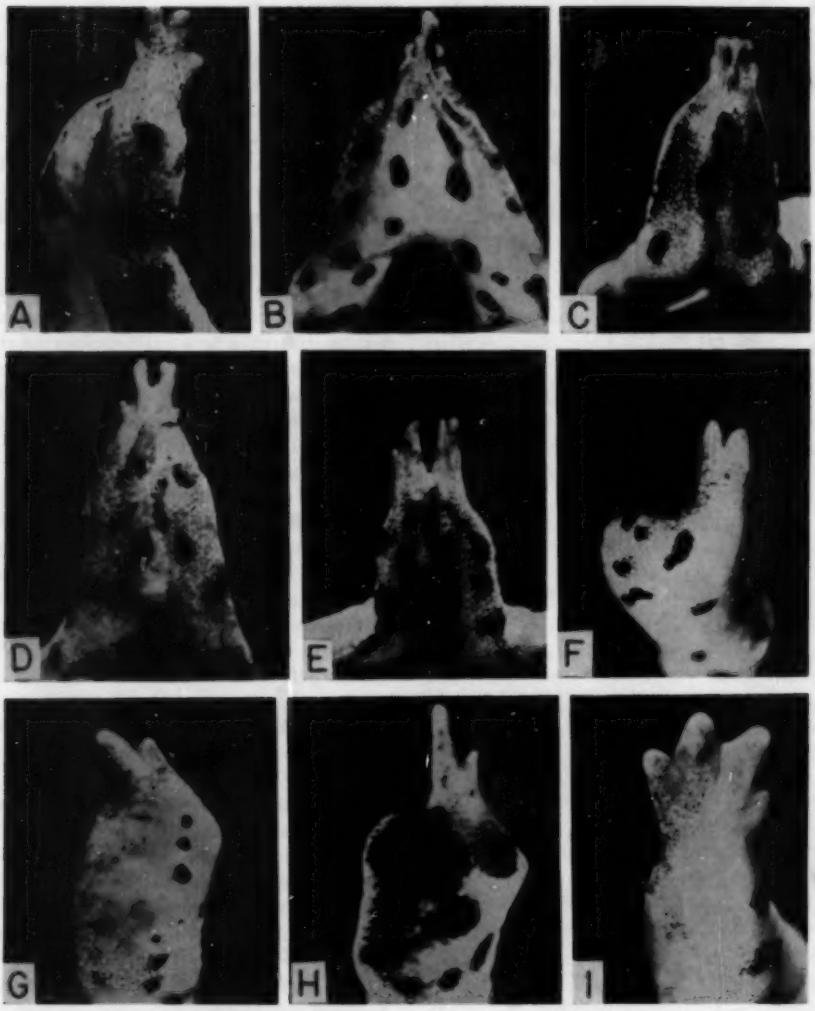

FIG. 5. REGENERATION FOLLOWING GRAFTING THE LOWER LIMBS OF *Triturus* TOGETHER OR AFTER PARTIAL EXPOSURES TO X-RAYS

A. Lateral posterior view of a completely single regenerate from two lower limbs; 7 weeks after operation. B. Double lower-limb regenerate comprising three single digits and a pair of double digits; 7 weeks after grafting two lower limbs together. C. Regenerate from two grafted lower limbs in which the first and second digits are double but the third and fourth are single; 7 weeks after operation. D. Duplicated lower limb regenerate from 2 grafted lower limbs, exhibiting unification of the most posterior digit (arrow) and duplication of the 3 anterior digits; 7 weeks after operation. E. Completely double regenerate produced by 2 grafted lower limbs which have not united intimately; 7 weeks after operation. (Goss, 1956b.) F. Regenerate produced by a limb after the posterior half of the mesoderm had been removed and the posterior skin had been irradiated; the X-rayed skin failed to bring about regulation in the defective mesoderm. G. An incomplete 2-digit regenerate produced as a result of irradiating the posterior half of the mesoderm while shielding the posterior skin; 8 weeks after operation. Unirradiated skin proved incapable of mediating mesodermal regulation when not in direct contact with regenerating tissues. H. Regenerate produced as a result of exposing the posterior half of a hind limb to X-rays; 8 weeks after operation. Regeneration from only the anterior unirradiated part of the stump has resulted in the production of half a foot with 2 digits. I. A complete regenerate produced from a hind limb after irradiating only the posterior half of the skin; 8 weeks after operation. This treatment failed to interfere with the normal morphogenesis of the regenerate. (Goss, 1957.)

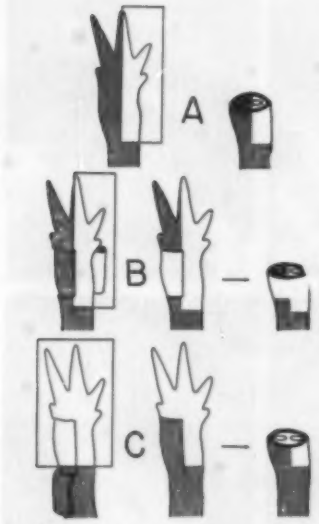

FIG. 6. DIAGRAMS ILLUSTRATING PARTIAL IRRADIATION OF AMPHIBIAN LIMBS WITH X-RAYS

A, half of the hind limb was irradiated; B, half of the mesoderm was irradiated while the corresponding skin was shielded; C, half of the skin was X-rayed but not the underlying mesoderm. Irradiated areas of limbs are shaded; unshaded rectangles indicate parts shielded from X-rays. (Goss, 1957.)

radiation, the limbs were amputated between the knee and the ankle. In other experiments, either the posterior mesoderm or the corresponding skin was irradiated.

In the first group (Fig. 6, B), the posterior skin was separated from the underlying tissues and was retracted anteriorly. The denuded posterior mesodermal half of the leg was then irradiated, but the anterior half, together with the posterior skin, was shielded. After exposure, the unirradiated skin was folded back over the irradiated mesodermal portion and was held in place by small sutures. The reciprocal experiment (Fig. 6, C) was done by folding the posterior skin back on the region of the more proximal thigh, irradiating the latter but shielding the shank, and then restoring the exposed skin to its normal position. In the last case, the limbs were normal, except that the skin covering their posterior halves had been irradiated.

The results of these experiments showed that when either the anterior or posterior halves of the legs are irradiated, regeneration occurs only from the unirradiated halves (Fig. 5, F–H). After the posterior half of the mesoderm was irradiated, incomplete regenerates were obtained. This demonstrated that unirradiated skin must be in contact with actively regenerating tissues in order to induce regulatory responses. If the posterior half of the skin alone was irradiated, complete regenerates were formed. Irradiated skin cannot suppress normal regeneration (Fig. 5, I).

Goss (1957b) explained the contrary finding of Lomovskaya (1948) as follows. The most important difference between her experiments and his own was that amputation of the treated extremity was done in her experiments one month after irradiation, rather than on the same day, as in his. It is significant that the complete regenerates obtained from such limbs grew from the entire stump, including the irradiated half. Goss (1957b) suggests that unirradiated cells migrated from the shielded side of the limb to the irradiated side prior to the beginning of regeneration. Such migration might be favored by injury to the limb at the time of irradiation, as well as by the long interval between irradiation and amputation.

It is necessary to note that Lomovskaya (1948) irradiated 36 animals, and normal regeneration was observed only in 15 cases. She did not describe what was observed in the others. I feel that the experiments of this author should be repeated. Perhaps these results can be explained on the basis of experimental error. In local irradiation, there is always the possibility that an animal may move the target limb out of the field, with the result that the limb escapes irradiation. I regard cell migration from the unirradiated portion to the irradiated as scarcely probable. Scheremetjewa and Brunst (1938) showed that the regenerative capacity of *Triton cristatus* can be suppressed by local simultaneous irradiation of the proximal and distal parts of a limb, but may be preserved in a thin intermediate section, if the latter is protected from irradiation (Brunst, 1950a).

THE REGRESSION OF REGENERATES

In my previous review (Brunst, 1950a), much attention was given to the phenomenon of reduction, resorption, or regression of irradiated regenerates. This phenomenon was observed by many investigators after X-ray irradiation of regenerates, or after destruction of the regenerate's

innervation (Schotté, 1926; Brunst, 1926; Butler and Schotté, 1941; Schotté and Butler, 1941; Trampusch, 1959; and others). In this section of the present paper, consideration is given only to new investigations of this process which verify previous conclusions concerning this very typical reaction of irradiated regenerates (Brunst, 1960, 1961).

During the regression, the regenerate undergoes gradual reduction from the distal end. The distal ends of the toes showed the first signs of reduction, and the toes gradually disappeared. When the process of reduction continued unabated, it extended proximally until dissolution of the regenerate was complete. The intensity of the reduction varied in different ahimals. In the adult axolotl (*Siredon mexicanum*), regression was observed in 90 per cent of the animals irradiated with 4000 r, and in 100 per cent of the animals irradiated with 6000 r. All toes disappeared within 60 to 80 days (Brunst, 1960).

During regression of the limb, the skin epithelium was greatly reduced, but the exact mechanism of this reduction remains obscure. My earlier opinion, that epithelial reduction occurred as a result of the lytic enzymes produced by macrophages located in immediate proximity to the epithelial cells (Brunst, 1950a), was not confirmed by the new investigation. Macrophages were rarely found in immediate proximity to epithelial cells, in spite of active degeneration of these cells. On the contrary, they were found near normal epithelium. Although there was no direct evidence of the mechanism of reduction of skin epithelium, contraction of the surface of the epithelium probably occurred earliest in places where it was unusually thin. The presence of large blood sinuses immediately beneath the epithelium may be important for this process. Such sinuses, never seen in normal animals, were formed from blood vessels damaged during regression. In any case, the absence of connective tissue support for the epithelium created favorable conditions for its contraction and reduction.

Resorption of the skeletal cartilage and bone is a result of the activity of macrophages. Regenerates with 4 toes had comparatively small and thin ossification (Fig. 7, A). A thin layer of bone usually covered the proximal end and distal portions of the cartilaginous skeletal element. The attack of the macrophages on this element always began at the surface, and often the peripheral bone layer was damaged first. In some cases, the bone layer was completely destroyed on one side, but hardly damaged on the other. Always the macrophages were located in close proximity to the bone surface (Figs. 7, D and 8). The cavities and holes in the bone and cartilage evidently resulted from the action of lytic enzymes secreted by the macrophages (Fig. 7, B and D). After a hole was formed in the bone layer, macrophages could penetrate into the cartilage. In such a case, the bone layer temporarily remained almost intact, whereas almost all the cartilage within was dissolved by macrophage enzymes and disappeared (Fig. 7, B).

The appearance of cartilage undergoing reduction was in great contrast to that of the normal cartilage of a control animal (Fig. 7, B and D vs. A and C, respectively). The number of cartilage cells was greatly reduced, and many macrophages were found in close contact with the cartilage and penetrating into it. Many small cavities appeared in the intercellular substance of the cartilage. These cavities later connected and transformed into one large cavity occupying almost the whole cartilaginous element. When reduction was complete, all macrophages disappeared. Reduction was not a continuous process in all cases, although the causes of its interruption are not known.

In the process of reduction, compact muscle bundles were transformed into isolated small thin muscle bundles, or even isolated muscle fibrils and separated muscles, which gradually disappeared. This process probably is connected with the activity of macrophages.

Early blood vessel damage was manifested in an increased number of small capillaries and vessels and in dilatation of the vessels. Advanced damage was characterized by disappearance of the blood vessel walls, with the formation of large sinuses, often immediately under the skin epithelium.

The most important phenomena in the process of reduction of regenerates are resorption of the skeleton as a result of the activity of macrophages, and destruction of the distal blood vessels. Soft tissues without skeletal support contract and are destroyed more easily by macrophages. As a result of blood-vessel damage, reduction occurs under conditions of abnormal blood supply, which may favor its advance. The resorption process is the result of reaction of the body to the damaged limb (as a result of ir-

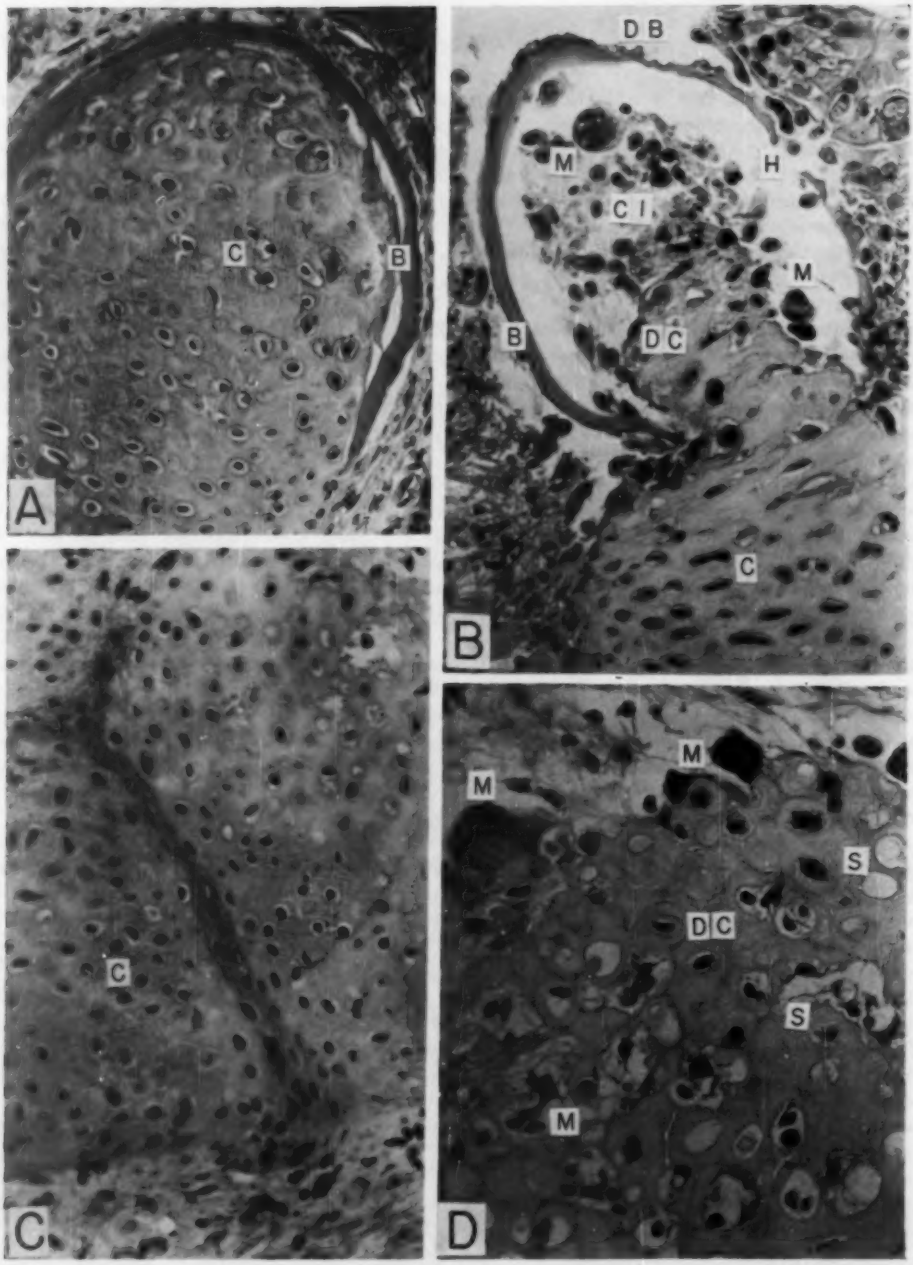

FIG. 7. THE REGRESSION OF REGENERATES IN THE AXOLOTL (*Siredon mexicanum*)
A. Normal limb regenerate of control animal: (B) exterior bone layer; (C) cartilage. Photomicrograph × 150. B. Limb regenerate of axolotl 63 days after local irradiation with 4000 r: (B) exterior bone layer partially damaged by macrophages; (DB) cavity in bone layer, formed as a result of macrophage activity; (CI) isolated cartilaginous nuclei left after both intercellular and intracellular substance have been dissolved; (C) cartilage, almost normal in appearance; (DC) cartilage undergoing reduction; (H) hole in bone layer; (M) macrophages. Photomicrograph × 150. (Brunst, 1961.) C. Normal cartilaginous tissue of a control animal: (C) cartilaginous cells. Photomicrograph × 160. D. Part of section through axolotl limb regenerate undergoing reduction, 64 days after local irradiation with 4000 r: (DC) damaged cartilage; (M) macrophages of various sizes; (S) empty space which results after cartilaginous substance undergoing reduction has dissolved. Photomicrograph × 160. (Brunst, 1961.)

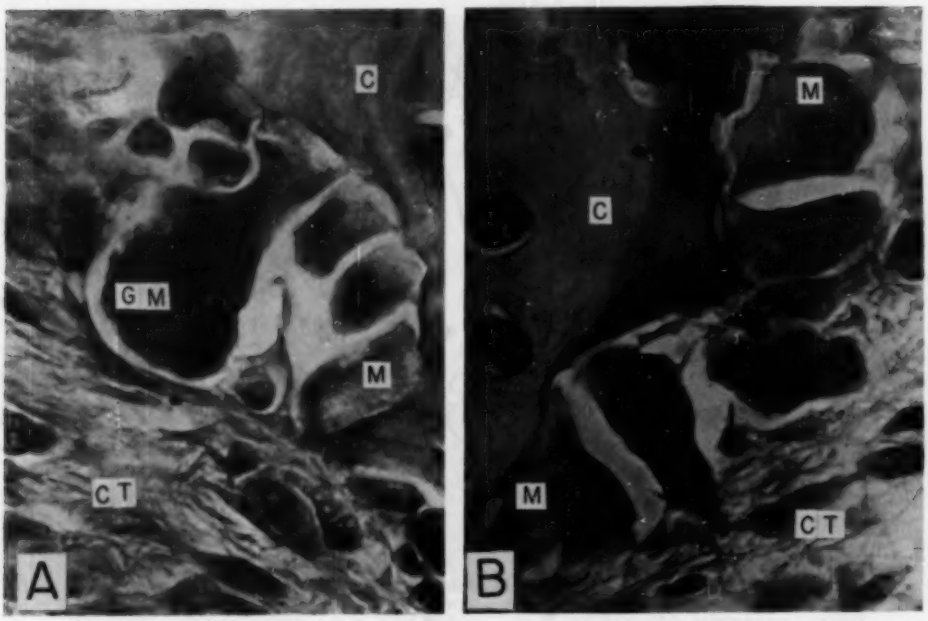

FIG. 8. THE REGRESSION OF REGENERATES
A. Regenerate of axolotl 63 days after local irradiation with 4000 r: (C) cartilage; (CT) connective tissue; (GM) giant macrophage; (M) macrophages. B. Regenerate of axolotl 126 days after local irradiation with 4000 r: (C) cartilage; (CT) connective tissue; (M) macrophages. Photomicrographs × 500. (Brunst, 1961.)

radiation, destruction of the nerve supply, or other causes). It can be considered an inflammatory reaction.

Butler (1933) and Puckett (1936) also observed resorption in *Ambystoma* larvae after irradiation, and Butler (1955) made similar observations after reversal of the proximo-distal axis of the limb of *Ambystoma punctatum* and *A. opacum*. They undoubtedly observed the same phenomenon as that described above (Brunst, 1950a).

REGENERATION UNDER ABNORMAL CONDITIONS

Butler (1955) investigated regeneration of the forelimb in larvae of *Ambystoma punctatum* and *A. opacum* after reversal of its proximo-distal axis. The operation of reversal was performed in the following manner: first a small pocket was made in the muscles just posterior to the shoulder region; then the forelimb was amputated at the carpal level, and the distal end of the limb was immediately inserted into the previously prepared pocket. After operation, the animals were immobilized with an anesthetic for a period of 10 to 24 hours. On healing, the limb became firmly attached to the body wall at its distal (carpal) end.

The second stage of the procedure was amputation of the limb slightly distal to the head of the humerus. Obviously the amputated carpal region, after healing in the body wall musculature, soon established vascular connections which became sufficient for the entire transplant. A week after operation, a period of regression of the nerveless reversed limbs began, starting at the free end of the transplant and progressing toward the body. It is necessary to emphasize that regression occurs in a distal direction with respect to the original polarity of the limb; i.e., proximal with respect to the orientation of the transplant. In most cases, the regression continued until all or nearly all of the humerus had disappeared (Fig. 9). After this, the regression ceased in most cases, probably because the reversed limb had become innervated. In 15 cases, however, regression continued, and the trans-

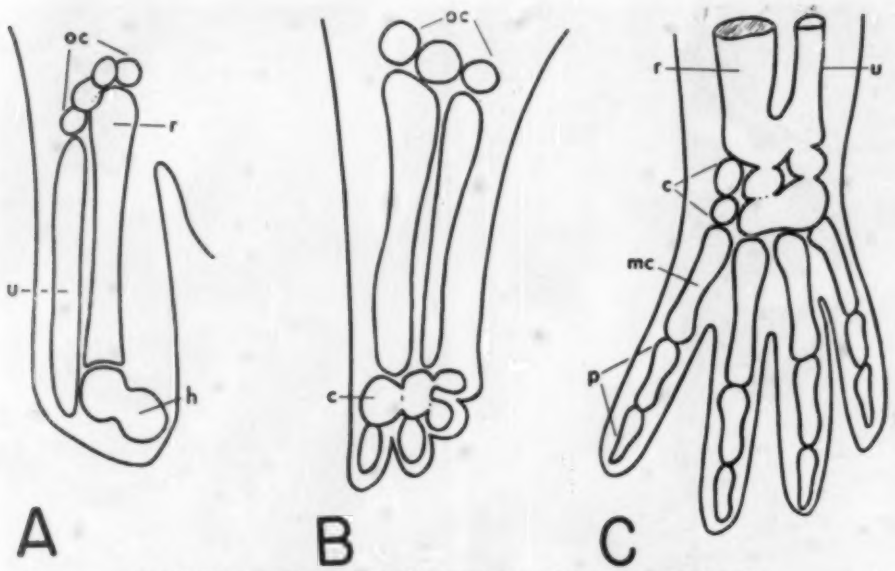

FIG. 9. THE RESULTS OF LIMB INVERSION IN *Ambystoma opacum* LARVAE

A. Graphic reconstruction of the skeleton of a reversed limb of an *Ambystoma opacum* larva. Point of attachment of limb to body wall is at the top; 4 of the original carpals (oc) are present. Limb has undergone regression so that only a small portion of humerus (h) remains, articulating with radius (r) and ulna (u). B. Graphic reconstruction of the skeleton of a reversed limb of an *Ambystoma opacum* larva; 3 of the original carpals (oc) are present. At the free end of the reversed limb, there has been established a regenerate in which new carpals (c) and the skeletal elements of 4 digits have been formed. C. Graphic reconstruction of the skeleton of hand and wrist of a reversed limb of an *Ambystoma opacum* larva. Original proximal ends of radius (r) and ulna (r) have fused. New carpals (c), metacarpals (mc), and phalanges (p) are present. (Butler, 1955.)

plant disappeared completely. Once regression has ceased, normal regeneration from the distal end of the transplant begins. The reversed limbs are much shorter than the normal, but they possess 3 or 4 well-formed digits (Fig. 10). Study of the skeleton showed that the skeletal elements have a tendency to fuse together in some cases (Fig. 9). The histological characteristics of regenerates are completely normal. Muscles are less well differentiated, but some slight movement was observed (Fig. 11).

It should be noted that in these remarkable experiments the lost structures have not been reproduced, and that new structures, not previously present, have been formed. Although in all cases the morphological circumstances of the reversed limb are highly abnormal, the structures which arise from the blastema are established in a completely coordinated manner. It may be possible to regard the regenerates which develop after amputation of reversed limbs as more or less comparable to accessory limbs. In each case, the structure results from an atypically situated blastema. Balinsky (personal communication, 1960) interprets the results of these experiments as follows:

> The regeneration of distal parts of urodele limbs from an originally proximal surface of a limb healed in a reverse orientation, far from being a paradoxical phenomenon, fits quite well in the general pattern of processes of regeneration. It has obviously some connection with restriction of regeneration capacity. In urodeles the regeneration capacity, although quite considerable, is not unlimited: the regeneration of a whole animal from the proximal cut surface of an amputated limb is entirely out of the question. The regeneration bud at a cut surface of a limb will produce parts of the limb, and nothing else. Each level in a limb, if given the opportunity to develop a regeneration bud, gives rise to the parts of the limb *distal* to the level at which the bud is formed. This is true independently of whether the distal portions of the limb had actually

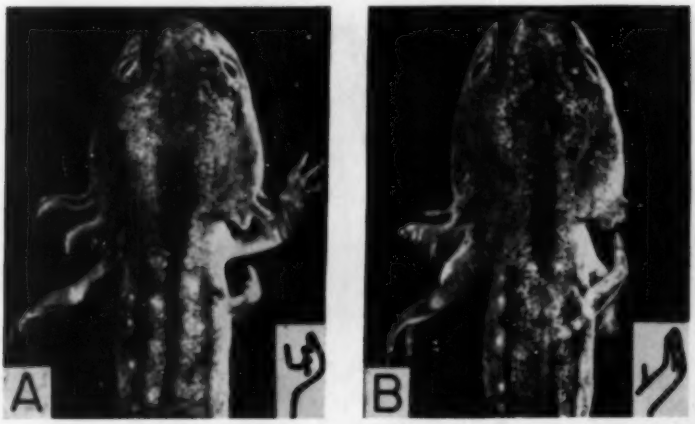

FIG. 10. PHOTOGRAPHS OF *Ambystoma opacum* LARVAE WITH REGENERATED REVERSED LIMBS
A. *Ambystoma opacum* larva 64 days after reversal; a 3-digit reversed limb. Normal right limb has completely regenerated. B. *Ambystoma opacum* larva 58 days after reversal; a 4-digit reversed limb. Normal right limb has completely regenerated. Right gills were amputated. (Butler, 1955.)

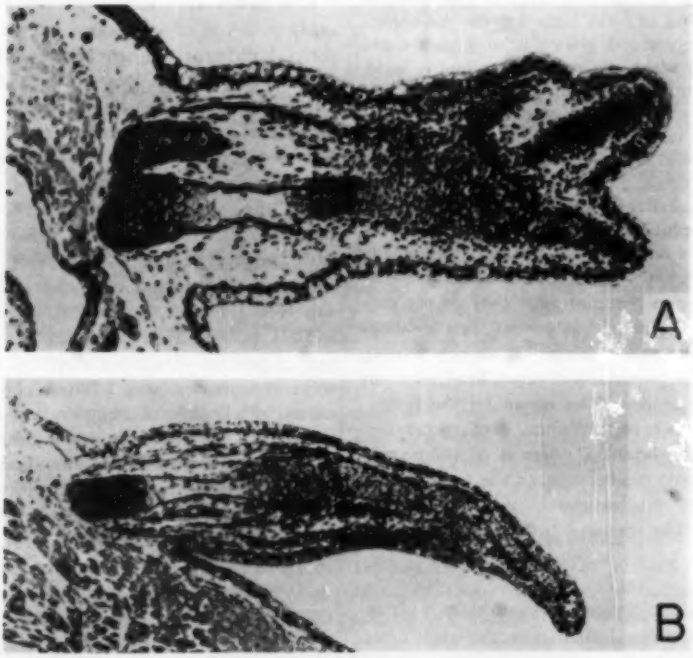

FIG. 11. SECTIONS THROUGH REVERSED LIMBS OF *Ambystoma opacum* LARVAE, SHOWING EARLY REGENERATES IN WHICH NEW CARTILAGE IS BEING DIFFERENTIATED
(Butler, 1955)

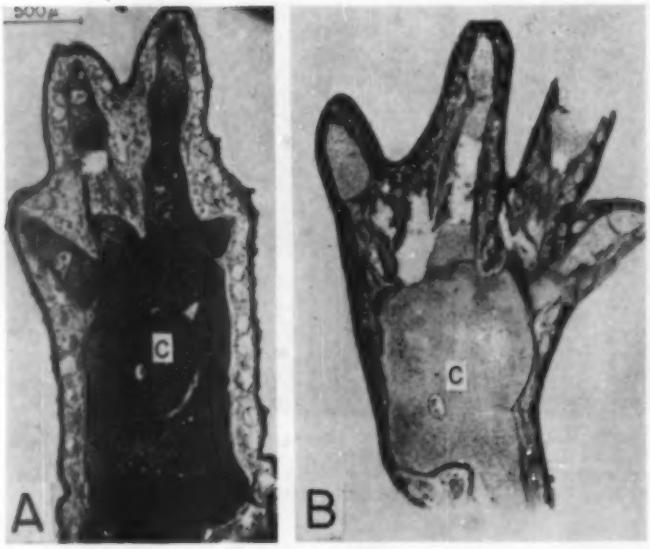

FIG. 12. FUSION OF SKELETAL ELEMENTS IN REGENERATES
A. Section through regenerate from *Triturus viridescens* limb transplant with reversed proximo-distal polarity. Darkly stained transplanted portions of radius and ulna can be distinguished from the more lightly stained bones of the regenerate. (Dent, 1954.) B. Section through paralyzed hind limb of *Triton cristatus*. (Brunst, 1927.)

been removed or not (as in experiments on superregeneration carried out by Nassonov, 1930–1936, and others). It is thus only natural that when a proximal surface of a cut limb is given the opportunity to regenerate it gives rise to a part distal to the level at which the regeneration bud is being formed. The level from which regeneration starts is determined by the position of the blastema in respect of the whole limb, but the outgrowth and differentiation is always outwards (in a distal direction).

Change of polarity in regeneration is by no means limited to amphibian limbs: cases of heteromorphic regeneration in earthworms and planarians show the same phenomenon. When very short pieces are cut at the anterior or posterior ends, they do not produce the missing parts, but instead there develops an approximate mirror image of the regenerating piece: a second, posteriorly directed, head, or a tail end pointing forward. The reason for the heteromorphosis seems to be the limitation of regeneration capacity: at the head end there is no competence for tail (or body) regeneration, or the latter is suppressed by the predominant competence for head regeneration. The reverse is true in the case of the tail fragment.

Dent (1954) investigated regenerates with reversed proximo-distal polarity in the adult newt, the limbs of which were amputated at various levels. He established that less regression of tissues occurred in the shorter transplants than in the larger ones, and attributed this phenomenon to better blood circulation in short transplants.

It is noteworthy that Dent (1954) had previously observed in some cases extensive fusion of skeletal elements in regenerates with reversed polarity (Fig. 12, A). It is very possible that these abnormal structures can be explained by the absence of normal movement in the regenerates. Very similar regenerates with fusion of skeletal elements were obtained by Brunst (1927, 1932) when the regenerates were paralyzed or the proximal skeleton had been removed. In both cases, normal function (movement) was absent, and extensive fusion of skeletal elements was observed (Figs. 12, B and 13).

Deck (1955) investigated regenerates with reversed proximo-distal polarity, and showed that some regenerates have 2 hands. This condition arises as a result of regeneration at both the carpal and the humeral ends of the implant, following insecure implantation. The regenerate, instead of being inserted into the body, is held in place only by fusion of skin to the body along the side of the limb (Fig. 14, b). According to Deck (1955), there were developed in some cases atypical regenerates consisting only of a single digit (Fig. 14, e) or several digits atypically formed (Fig. 14).

Goss (1956c) investigated the response of the adult *Triturus* forelimb to amputation and insertion through the body wall into the body

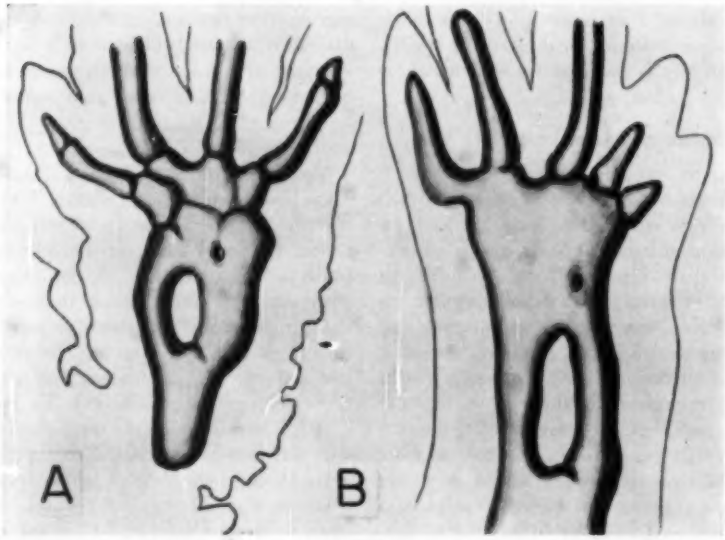

FIG. 13. GRAPHIC RECONSTRUCTIONS OF REGENERATED LIMBS OF *Triton cristatus*
A. Regenerate after extirpation of humerus. B. Regenerate after destruction of motor neurons of hind limbs in spinal cord. (Brunst, 1932.)

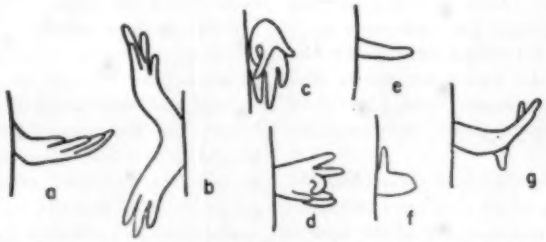

FIG. 14. SKETCHES OF REGENERATES AFTER REVERSAL OF PROXIMO-DISTAL POLARITY
a. Dorsal view: reversed forearm and regenerated hand. b. Ventral view: double regenerate, 4 digits on reversed forearm, 3 on regenerated forearm. c. Dorsal view: only 2 hands, 3 digits on each. d. Dorsal view: regenerate with single large hand and 6 digits. e. Dorsal view: a single oversized digit. f. Dorsal view: an implant with smoothly rounded distal tip and a single digit extending from the body wall. g. Dorsal view: a slender stump with 3 digits fanning out radially at distal tip. (Deck, 1955.)

cavity. The response of both normal and skinless amputated limbs to these conditions has been studied. It has been shown that limb stumps are incapable of regeneration when inserted into the body cavity, because of their inability to produce adequate terminal accumulations of blastema cells. When the skin of the lower arm was left intact, it underwent progressive degenerative changes in the body cavity —such stumps responded as did skinless ones.

Goss (1956d) inserted skinless forelimbs of adult *Triturus* into the body cavity, 1, 2, or 4 days after amputation, and found that such limbs did not regenerate when they were inserted so soon. If insertion was delayed 6 days, however, some regeneration occurred in some cases. After a delay of 2 or 3 weeks, regeneration was abnormal but quite extensive. Obviously, skinless intracoelomic limb stumps cannot regenerate unless blastema formation has been started previously. The limb stumps with skin intact, which do not regenerate when inserted immediately into the body cavity after amputation, produce well-developed regenerates if in-

sertion is delayed 1 or more days. This delay permits epidermal wound healing of the stump, which apparently is essential for the initiation of limb regeneration.

ABNORMAL REGENERATION

According to the usual definition, regeneration is the replacement of lost parts. This definition, however, is not applicable in all cases. In some of the cases described in the preceding section, it was entirely inapplicable. According to Schaxel (1921), even in cases of simplest regeneration with very smooth amputation surfaces, the regenerate is not an exact replica of the lost portion. Some degree of atypia is always observed. The regenerates differ in various details of structure from the corresponding portion of the body that existed before the amputation.

Under the circumstances, it would be better not to define regeneration as replacement of a lost part, but as formation of a portion only more or less similar to the portion that existed before amputation. For example, the experiments of Schaxel (1921) showed that new skin, regenerated following extirpation of a portion, is atypical in the axolotl. The epidermis has a very small number of Leydig's cells; in the dermis, large multicellular glands are absent; and the distribution of connective tissue fibers is irregular. Only a few blood vessels and nerves are present.

After amputation of the tail of the axolotl, the regenerate has an atypical structure. Metamerism, which is highly characteristic of the normal tail, is expressed only very slightly. This is especially clear in the structure of the blood vessels. Typically, the segmental blood vessels branch from the main longitudinal blood vessel (Fig. 15, B). In the regenerate, the structure is completely different: almost all blood vessels run parallel to the longitudinal axis of the regenerating tail (Fig. 15, A).

In regenerates of extremities (Schaxel, 1921), slight malformations, such as fusion of digits (Fig. 15, C and E), are frequent. Even "normal" regenerates, however, are atypical in details of structure, such as position and size of digits, distribution and position of blood vessels and nerves, and differentiation of the skeleton (Fig. 15).

One fact that is very important to consider is that it is not the absence of an organ but the presence of a wound that acts as the stimulus for regeneration (Balinsky, 1960). Therefore, if the wound is uneven or incorrectly made, or involves several sides of the organ (e.g., a limb), one stump may develop into many incorrect limbs or tails. This is abnormal regeneration or super-regeneration.

Many amphibians with natural super-regeneration have been found in nature. Tornier (1898) described a frog (*Rana esculenta*) with 4 forelimbs: 1 normal limb on the left side, and 3 limbs on the right (Fig. 16, B). Anatomical investigation by this author showed that this malformation was the result of super-regeneration from a broken scapula. The two halves of the scapula were separated, and regeneration occurred from both portions.

It is interesting that the same author obtained very different forms of super-regeneration in the extremities of the frog *Pelobates fuscus* under experimental conditions (Tornier, 1905). The operations were performed on the extremities in a very early stage of development, when the limb buds in tadpoles are very small. This early anlage was cut with scissors longitudinally on each side of the body.

It should be noted that Tornier's surgical cut was deep enough to damage the pelvic girdle, or in some cases even to snip it. As a result of damage and contraction of the tail muscles, the borders of the wound were separated. Each wound surface started a separate regeneration process. The isolated portions of the pelvic girdle or limb skeleton formed the new additional limbs as a result of the regeneration process. According to Tornier (1905), growth of the regenerate is proportional to the size of the wound.

Perhaps the most interesting result of such operative interference in the normal formative process is Tornier's tadpole with 6 hindlimbs (Fig. 16, G and G_1). This tadpole is very close to metamorphosis, but still has a normal tail. The adult frog, with 4 hind legs, is shown in the next picture (Fig. 16, I). Another frog has 5 hind legs. It should be noted that two of the right limbs in this case are not completely separated (Fig. 16, K). In another case (Fig. 16, L), Tornier also observed incomplete separation of an additional leg and consequently the formation of a fused tarsus with 8 toes. The frog with a normal left limb and a very complicated right limb is also a result of incomplete separation of additional legs (Fig. 16, H). A similar but less

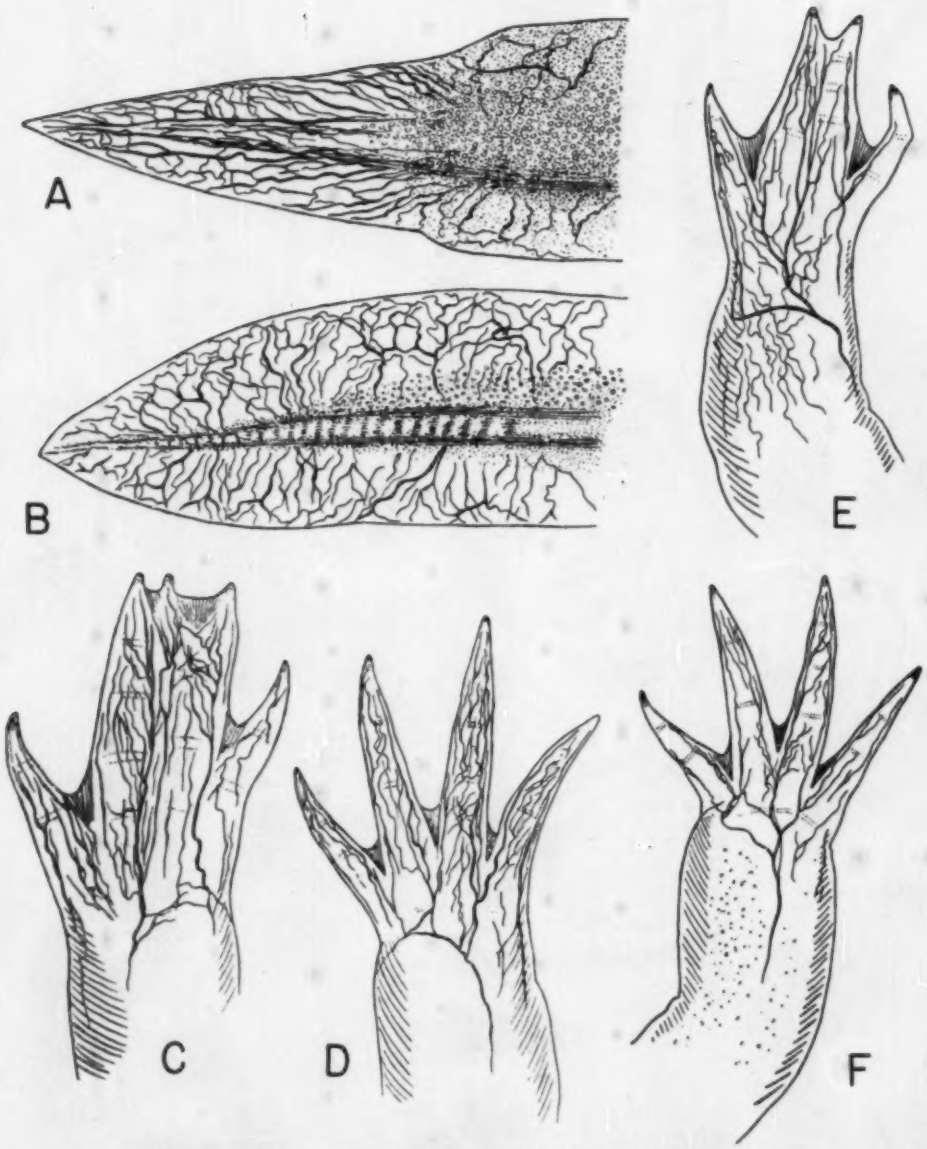

FIG. 15. ATYPICAL STRUCTURE OF REGENERATES IN AXOLOTL (*Siredon pisciforme*)
A. Structure and distribution of blood vessels in regenerates of the tail. B. Normal structure and distribution of blood vessels in a normal tail. C. Abnormal regenerate of left limb, with fusion of 2 digits and atypical structure of blood vessels. D. Normal structure of right limb of the same animal as in C. E. Abnormal regenerate with fusion of 3 fingers. F. Normal right limb of the same animal as in E. Note the similarity in the structures of the typical adult limbs in D and F. (J. Schaxel, 1921.)

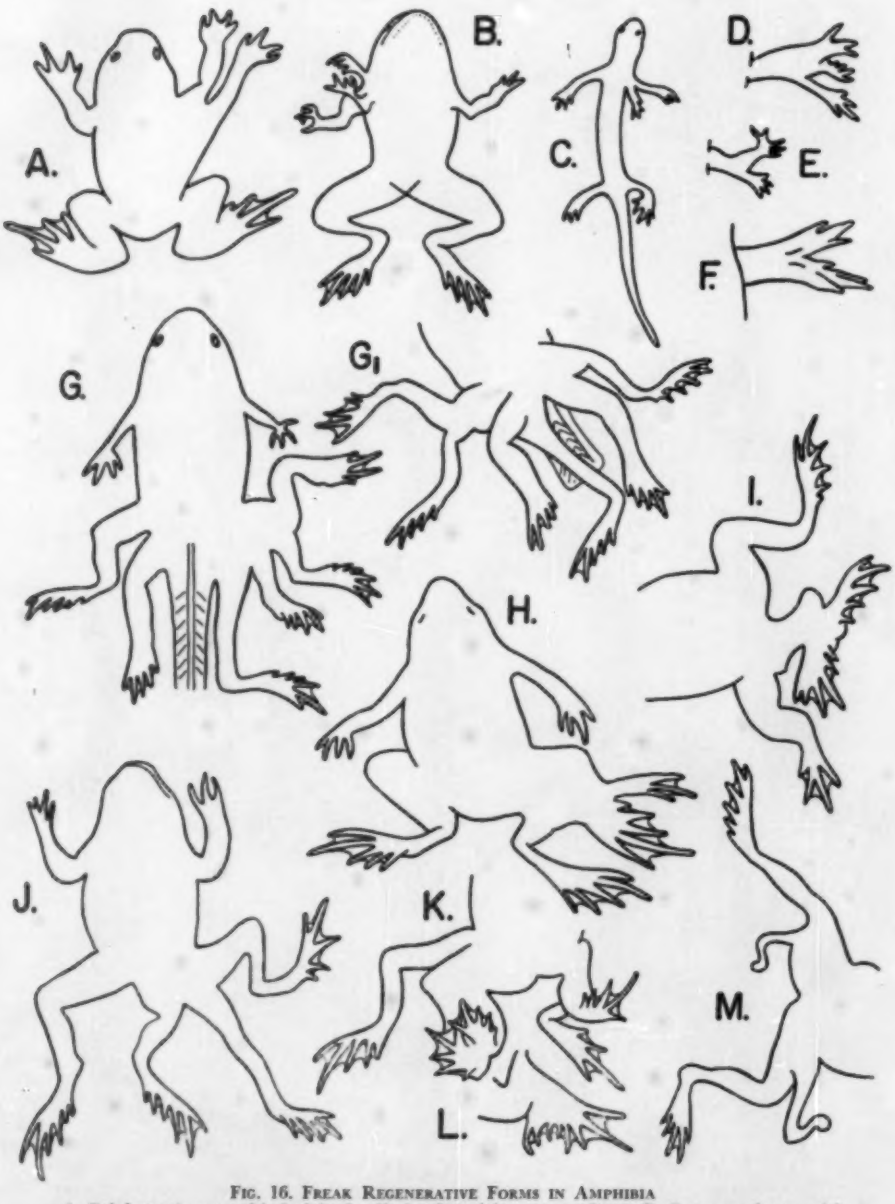

FIG. 16. FREAK REGENERATIVE FORMS IN AMPHIBIA

A. *Pelobates fuscus*, with 2 right forelimbs; found in nature (Otto). B. *Rana esculenta*, with 3 right forelimbs; found in nature (Tornier). C. *Triton taeniatus*; found in nature (Barfuth). D and E. *Siredon pisciformis*, showing results of damage by bites of other animals (Dumeril). F. *Triton cristatus*, showing results of damage by bite of another animal (Tornier). G–M. Experimental super-regeneration in frog *Pelobates fuscus*, resulting from operations performed on tadpoles by Tornier. (Przibram, 1921.)

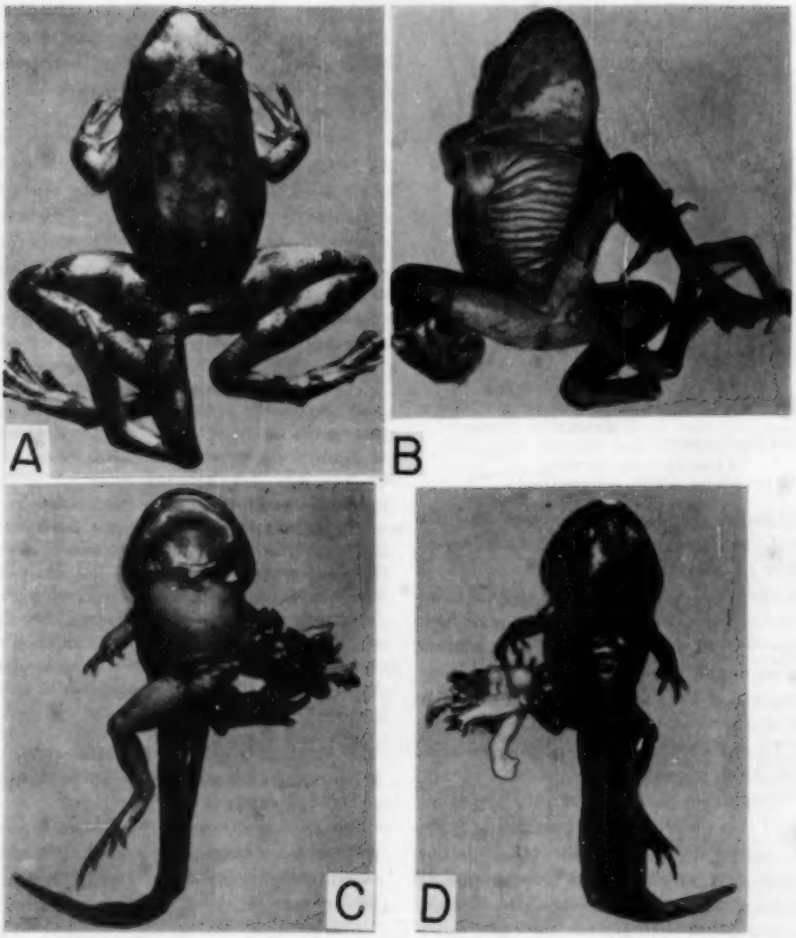

FIG. 17. SUPER-REGENERATION IN FROGS AND TADPOLES FOUND IN NATURE
A. Frog with 1 additional hind limb. B. Frog with 2 additional hind limbs. C and D. Tadpole with greatly malformed regenerate of left hind limb. (Hellmich, 1929.)

complicated case is shown in Fig. 16, J. Finally, the last animal is interesting, because each leg has an accessory rudimentary leg connected with the main limb in the femoral region (Fig. 16, M).

The experiments of Tornier are very important, because they explain the origin of the freak forms observed in nature (Przibram, 1921; Hellmich, 1929; and others; Figs. 16 and 17). All of these forms are results of damage and subsequent super-regeneration. Some of the forms found in nature are very complicated; e.g., a very interesting tadpole of *Alytes obstetricans* (Hellmich, 1929), with a giant regenerate consisting of 12 separate limb anlages (Fig. 17, C and D).

In the last case, the hindlimb of the tadpole was, obviously, very badly bitten by other animals. In most cases, the cause of super-regeneration occurring in nature is damage due to bites by other animals. For example, adult newts willingly eat small larvae of amphibia. It is possible that a frightened newt will abandon a damaged larva. In most cases, of course, the

FIG. 18. SUPER-REGENERATION OF DIGITS OF A NEWT (*Triton cristatus*) AS A RESULT OF DOUBLE AMPUTATION (CROSS SECTION AND LONGITUDINAL SECTION)
(P. Weiss, 1925b, schematized.)

damaged larvae die; but in rare cases they survive, and the damage is followed by super-regeneration (Brunst, 1937).

Laboratory observations confirm this explanation in many cases. Bites by other animals have been observed to produce complicated wounds and subsequent super-regeneration. Such developments have been described as occurring in axolotls (*Siredon pisciforme*; Przibram, 1921; Fig. 16, D and E) and newts (*Triton cristatus*; Przibram, 1921; Fig. 16, F).

The direction of the amputation plane is important. If it is oblique in relation to the longitudinal axis of the limb or the tail, super-regeneration may occur. If the amputation is oblique all the way across the limb, or if digits are snapped off on both sides of the limb, super-regeneration may produce many digits. Weiss (1925b) performed two types of amputations on the limbs of the newt (*Triton cristatus*): cross section and longitudinal section. Consequently, two wound surfaces and two independent regeneration blastemas were formed. From the cross section, regeneration was normal, and a regenerate with 4 or even 5 digits was formed in spite of the small amputation surface. The regeneration blastema from the longitudinal section never replaced the amputated portion, however, but formed many separate digits, often very close to one another (Fig. 18).

Implantation of a tumor (adenocarcinoma) into the stump of a limb of the axolotl (*Siredon mexicanum*) provokes in many instances the formation of many extra digits irregularly distributed on the surface of the tumor, obviously as a result of splitting of the regeneration blastema (unpublished observation by E. A. Sheremetieva-Brunst).

According to Balinsky (1960), the presence of an open wound is not always necessary for regeneration; the stimulus initiating regeneration need not involve amputation. This fact was demonstrated by the work of Nassonov (1930). The latter investigator tied ligatures around the extremities of axolotls. These ligatures caused considerable destruction of the tissues immediately affected by the pressure.

> "The muscles and portions of the limb disintegrate, so that the part of the limb distal to the ligature becomes bent at an angle and is dragged about by the animal without being capable of movement of its own. The skin, however, turns out to be more resistant, and preserves its integrity. After some weeks the region of the limb just proximal to the ligature begins to swell, and it soon becomes evident that a regeneration blastema has been formed. The regeneration blastema then develops into the distal part of a new limb, although the old distal part of the limb is still present. With the processes of differentiation setting in, the skeleton of the old distal part of the limb may be joined again to the proximal skeleton" (Balinsky, 1960).

As a result of ligation, super-regeneration may occur, and 3 or 4 additional limbs, often irregular, may develop (Fig. 19).

Super-regeneration in the absence of amputation has been observed in a young axolotl subjected to X-ray irradiation in the proximal portion of the tail, very close to the lumbo-sacral region (Brunst, 1950b). For example, in an animal fixed 203 days after irradiation with 1500 r (Fig. 20), 4 asymmetrical hindlimbs were formed. The anterior pair included a large left limb with normal development, but the right limb had not developed properly. The posterior right limb was correctly developed, but the corresponding left limb never appeared. In the median plane behind the anus, there was another posterior limb, which, in spite of its small size, had 5 toes. A reconstruction of the skeleton of this animal (Fig. 21) shows that only 2 limbs have normal development and differentiation (Fig. 21, 2 and 3). The anterior right limb (Fig. 21, 1) had only one skeletal element. The most posterior limb (Fig. 21, 4) had a normal skeleton distally, but the more proximal skeleton was abnormal, with

shortening and fusion of many elements. The pelvic girdle of the extremities was abnormal and asymmetrical (Brunst, 1950b).

It is clear that initiation of the regeneration process requires damage to the tissues of an organ that is capable of regeneration. In most cases, the damage is due to an open wound; but if extensive damage to the tissues can be produced without an open wound (e.g., by ligature or X-rays), this may be sufficient to start the sequence of processes leading eventually to regeneration (Balinsky, 1960).

"Having reached so far we may suggest that damaging the tissues is necessary so that some substance or substances be released from the damaged and disintegrating tissues, which are the immediate cause of the processes that follow. Various types of experiments have been adduced in support of this concept. It has been found that if a regeneration blastema of an axolotl limb is dried at low temperatures, so that the cells of the blastema are all killed, and this is then transplanted under the skin of an axolotl limb, it causes an outgrowth on the surface of the host limb, covered by skin and with a cartilaginous axis in the middle, comparable to a very rudimentary limb or at least to a digit. A similar outgrowth may be caused by an implanted piece of cartilage and also by introducing under the skin the products of alkaline hydrolysis of cartilage (Nassonov, 1936). These experiments immediately remind us of the experiments on the primary organizer in early amphibian development; there as here it was found that the stimulus for causing certain morphogenetic processes was not necessarily dependent on the integrity and vital activity of the cells of the inducing part, and that non-living substances could exert a similar action" (Balinsky, 1960).

"Another line of research consists in the treatment of the amputation surface with a solution of beryllium salt (beryllium nitrate). Beryllium nitrate applied to the amputation surface of a tadpole tail or of the limb of an *Ambystoma* larva completely suppresses regeneration (Needham, 1941, 1952). It has been suggested that beryllium in some way binds the substance released from the damaged cells at the wound surface that would have normally initiated the whole sequence of the processes of regeneration —the dedifferentiation in the first place and subsequently the formation of the regeneration blastema. Such an interpretation is supported by the following details of the experiments with beryllium. First, the beryllium treatment must be carried out immediately after the amputation; an hour later the treatment is without any effect. This might mean that the substances released from the damaged cells have already started off the next step of the reaction (the processes of dedifferentiation) or at least created the conditions in which this next step inevitably follows. Second, if after treatment of the wound surface the stump is again amputated 0.5 mm proximal to the original cut, regeneration proceeds normally. Thus the action of the beryllium is only very local. If new cells are damaged they may in their turn release the same substances and 'trigger off' regeneration. The treatment of normal tissues prior to amputation does not have any effect either; it is only after the cells are damaged that beryllium can in some way affect the results which could have been produced by the damaged cells. In this respect there is a profound difference between the inhibition of regeneration by X-rays and the inhibition of regeneration by beryllium nitrate. X-rays make the cells incapable of growth and reproduction, and this makes regeneration impossible. The demolition processes are not checked by the rays. On the other hand, beryllium does not impair the ability of cells to grow and differentiate, but it checks all the stages of regeneration by preventing the initial steps of regeneration from occurring. It

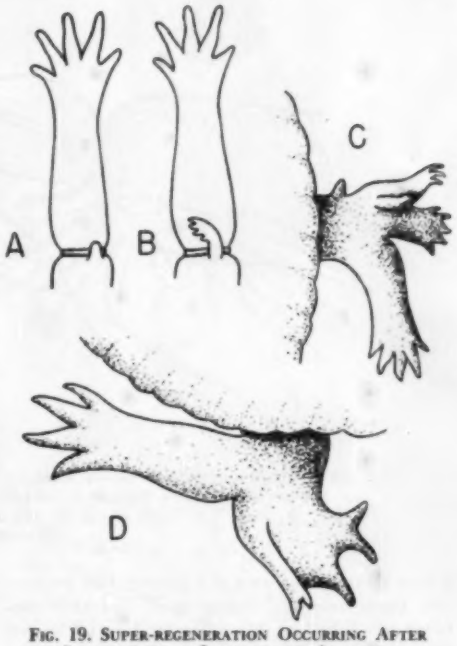

FIG. 19. SUPER-REGENERATION OCCURRING AFTER LIGATION OF A LIMB OF AN AXOLOTL, WITHOUT AMPUTATION

A. Initial development of limb bud in the proximal region of the extremity near the ligature. B. The same animal after 2 months. C. Super-regeneration 13 months after ligation. D. Super-regeneration 10 months after ligation. (Nassonov, 1930; Brunst, 1952.)

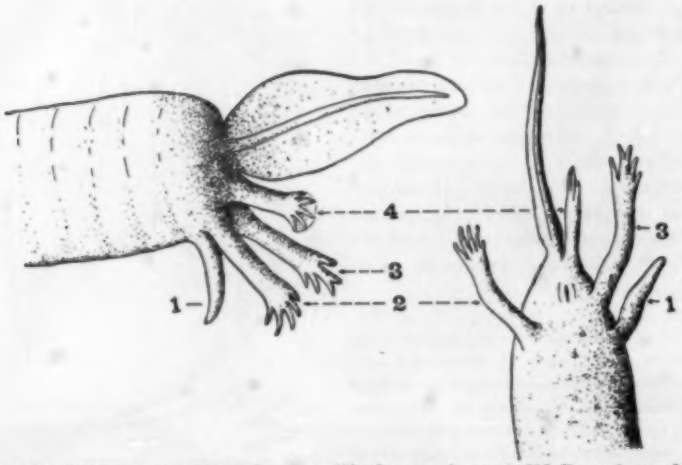

FIG. 20. SUPER-REGENERATION IN AN AXOLOTL (*Siredon mexicanum*) 203 DAYS AFTER LOCAL IRRADIATION OF THE PROXIMAL SECTION OF THE TAIL WITH 1500 r OF X-RAYS VERY CLOSE TO THE LUMBO-SACRAL REGION
(Brunst, 1950b.)

is thus very probable that it interferes with the specific factor releasing regeneration, and that this factor is a substance or substances given off by the damaged cells at the wound surface" (Balinsky, 1960).

STIMULATION OF REGENERATION AND POSSIBILITIES OF REGENERATION IN MAMMALS

It is important to know whether it is possible to excite regeneration in organs or organisms which do not normally regenerate (Balinsky, 1960). The legs of adult tailless amphibia (Anura) do not regenerate. According to Polezhayev (1946, 1958), the ability of the legs of tadpoles to regenerate suddenly disappears in the course of a few days. At a later stage, when the cartilaginous skeleton of the limb is fully differentiated, an amputated leg does not regenerate. Regeneration may be induced after amputation, however, if the stump is traumatized by sticking a needle into it several times. After this treatment, regeneration occurs normally, whereas a control limb on the same animal, not damaged by a needle, does not regenerate (Fig. 22). Histological investigation has shown that differentiation proceeds normally in the control limb, but many tissue cells are destroyed or damaged in the stimulated limb, and that this situation results in dedifferentiation of tissues, followed by formation of a regeneration blastema (Polezhayev, 1946, 1958).

Anuran limbs that do not normally regenerate can be induced to do so by applying solutions of various chemicals, e.g., glucose, salts, iodine, or nitric acid (Polezhayev, 1958). In the adult frog, amputation of the leg, followed by treatment of the wound with hypertonic salt solution, may cause regeneration (Rose, 1942, 1944). The same effect may be produced by transplanting tadpole skin (Gidge and Rose, 1944). Regeneration in adult frogs is also possible if an additional nerve is placed under the surface of the wound (Singer, 1954).

In mammals, regenerative ability is limited to tissue regeneration; that is, to the healing of defects and lesions in various tissues, but not to the restoration of lost organs (Balinsky, 1960). Nevertheless, not all the tissues are able to regenerate in mammals. For example, the bones of the extremities are able to regenerate, but not the bones of the adult skull. It is for this reason that defective portions of the skull are usually replaced with metal or plastic plates. The bones of the skull regenerate well in young dogs, cats, and rats, but not in the adult animals (Polezhayev, 1958). Especially important in the regeneration of skull bones is the dura mater (the hard connective tissue membrane of the brain); periosteum is not necessary.

Regeneration has been induced in adult mammals by implanting "sawdust" made from skull

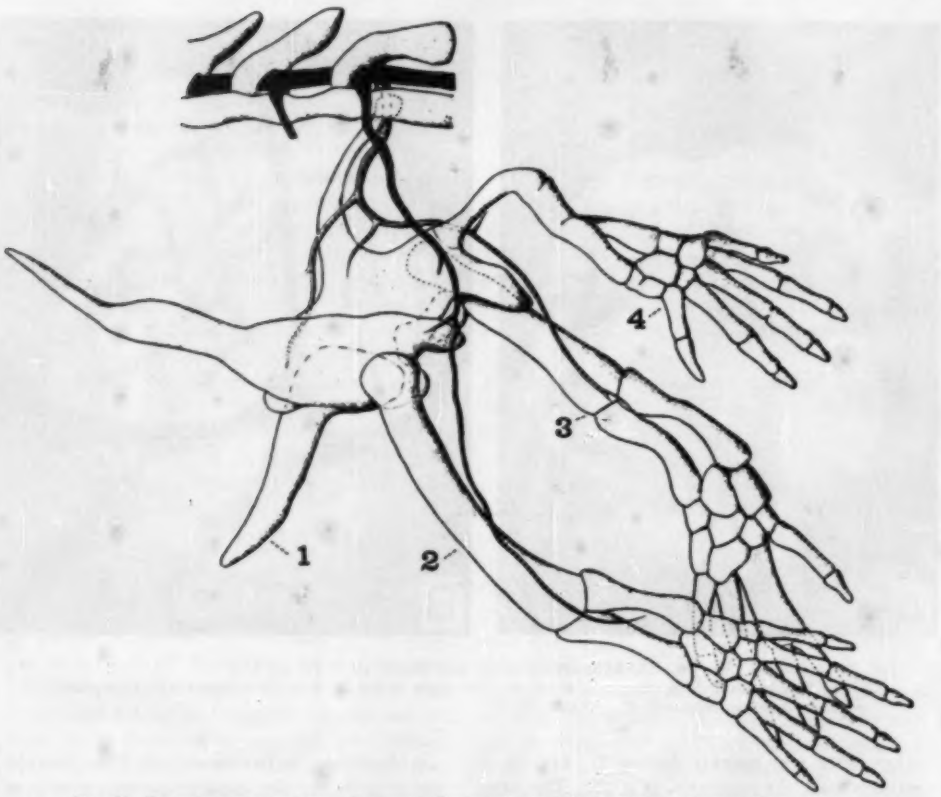

FIG. 21. RECONSTRUCTION (FROM SAGITTAL SECTIONS) OF THE SKELETON, SPINAL CORD, AND SOME OF THE NEURAL TRUNKS IN THE LUMBO-SACRAL REGION OF THE ANIMAL SHOWN IN FIG. 20
(Brunst, 1950b.)

bones into the cavities of bone defects. Excellent regeneration has occurred in 100 per cent of the instances where this procedure has been used. It is said that this method can be applied to human beings with similar success (Polezhayev, 1958). A similar method was utilized to stimulate regeneration of the dentine in the teeth of dogs. In 100 per cent of the cases, the dentine sawdust was transformed into a bonelike material (Polezhayev, 1958).

Although the brain does not regenerate in adult animals, excellent regeneration in brain defects has been reported by Polezhayev (1958) to occur in young dogs, cats, and rats. This regeneration occurs, however, only in the presence of brain membrane and in the absence of blood clots in the region of the wound. The process

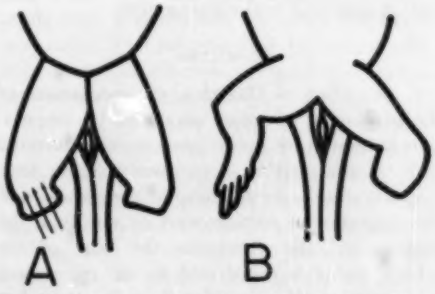

FIG. 22. STIMULATION OF REGENERATION IN A FROG BY TRAUMATIZATION

A. Traumatization of the right hind limb by sticking a needle into it several times. B. Normal regeneration in the stimulated limb and absence of regeneration in the opposite limb of the same animal; view from the ventral side. (Polezhayev, 1958.)

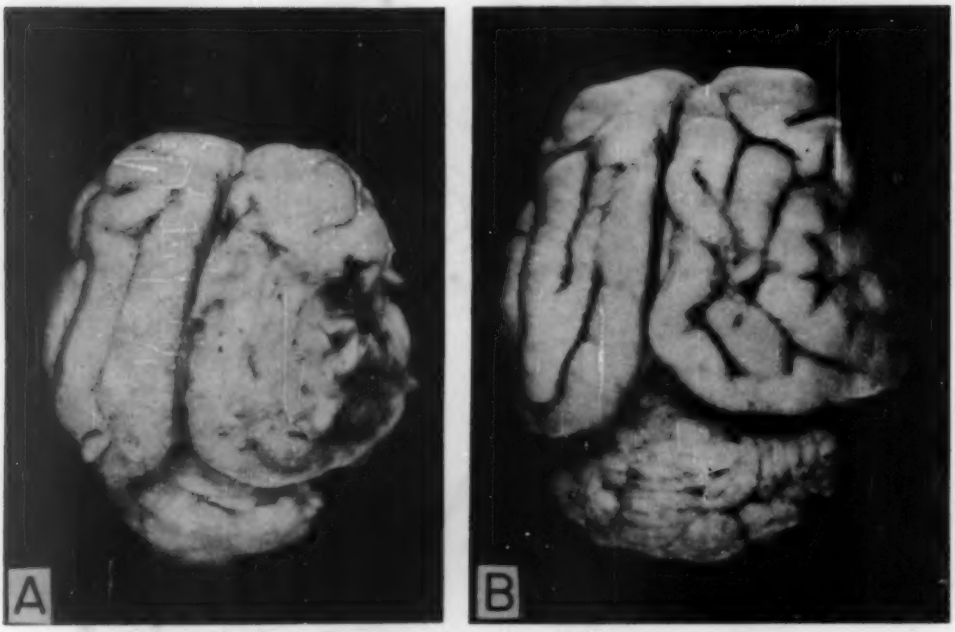

FIG. 23. REGENERATION OF THE BRAIN IN A YOUNG CAT
A. The brain 2 days after operation. B. The same brain 60 days after operation. Complete regeneration has occurred. (Polezhayev, 1958.)

takes place very quickly during the first 60 to 90 days after the operation (Fig. 23). The nervous tissue grows from the bottom of the wound to the top, the exact pattern of growth depending on the arrangement of the nerve fibers. The function of the brain after regeneration is normal (Kogan and Ivannikova, 1955).

SUMMARY

1. According to Chalkley, the mechanism of the healing of a wound produced by amputation (migration of epithelium) is not connected with mitotic activity. A mitotically active zone migrates distally from stump to regenerate, and this migration is accompanied by a shift in the number of cells. Gradually the peak of the mitotic index is transferred to the regenerate. The initial cell migration contributes a few thousand cells during the first 3 or 4 days. Migration of mitotically produced cells from stump to regenerate produces about 60,000 cells. Division of cells in the regenerate produces about 100,000 additional cells.

2. According to Godlewski and Rose, the epithelial cells are the most important source of the cells of the regeneration blastema. On the other hand, Chalkley, Manner, Heath, Brunst, and Weiss have shown that this assumption is not correct. Nevertheless, Polezhayev and Faworina, and Morosow, showed that the skin might play an essential role in manifesting the regenerative ability of the mesodermal portion of the amphibian limb. Goss demonstrated that the regulatory capacity of the regenerating limb is dependent upon the presence of a full complement of skin on the stump.

3. Bischler, Weiss, and others have shown that regeneration does not depend on the presence of bone in the region of amputation. Normal regeneration can occur from boneless regions, and the regenerates contain cartilaginous skeleton, which forms distal from the level of amputation. Goss, however, showed that implantation of extra bones in the limb, followed by amputation through the treated region, leads to the production of corresponding supernu-

merary skeletal elements in the regenerate. This paradoxical observation indicates that the blastema can regenerate skeletal elements not present in the stump, and can also form extra ones if additional bones are present in the stump.

4. X-ray irradiation is an especially important tool for investigating regeneration. Lomovskaya observed normal regeneration after irradiation of tibial or fibular halves. Goss, however, established that when either the anterior or posterior halves of the legs are irradiated, regeneration occurs only from the unirradiated halves. He suggests that in Lomovskaya's experiments unirradiated cells may have migrated from the protected side, because the amputation was done 1 month after irradiation. Possibly Lomovskaya's results also can be explained on the basis of experimental error, since cell migration from the unirradiated portion is not at all likely.

5. The reduction, resorption, or regression of regenerates can be observed after destruction of their innervation (Schotté, Butler and Schotté, and Trampusch) or after irradiation (Brunst). The most important phenomena in the process of reduction are resorption of the skeleton as a result of the activity of macrophages, and destruction of the distal blood vessels. Soft tissues without skeletal support contract and are more easily destroyed by macrophages. Damage to the blood vessels results in an abnormal blood supply, which may favor the progress of reduction. The resorption process is due to the reaction of the body to the damaged limb.

6. Butler investigated the regeneration of urodele forelimbs after reversal of their proximodistal axis. These remarkable experiments showed that although the morphological circumstances of the reversed limbs are highly abnormal in all cases, the structures which arise from the blastema, even in a direction opposite to normal, are established in a completely well-coordinated manner. Dent observed great fusion of skeletal elements in some regenerates with reversed polarity. Quite possibly these abnormal structures can be explained by the absence of normal movement in the regenerates.

Goss showed that skinless intracoelomic limb stumps cannot regenerate unless blastema formation has previously been started. Limb stumps with the skin intact do not regenerate when inserted into the body cavity immediately after amputation, but produce well-developed regenerates if insertion is delayed for 1 or more days. This delay permits the wound in the stump to undergo epidermal healing, which obviously is essential for the initiation of limb regeneration.

7. Regeneration is not exact replacement of a lost portion. Regenerates may differ in various details of structure from the original portion of the body that existed before the amputation (Schaxel). It is the presence of a wound that acts as the stimulus for regeneration. When the wound is incorrectly made or complicated, super-regeneration may be observed. The stimulus for regeneration need not involve amputation. For example, Nassonov tied ligatures around the limbs of axoloti. This resulted in considerable destruction of tissues, followed by super-regeneration. Super-regeneration in the absence of amputation also can be observed after local X-ray irradiation (Brunst). Some unidentified substances released from the damaged and disintegrating tissues are the immediate cause of dedifferentiation and the formation of a regeneration blastema. An outgrowth with a cartilaginous axis in the middle may develop after implantation of a piece of cartilage or dried regeneration blastema. Beryllium nitrate applied to the amputation surface completely suppresses regeneration (Needham), because in some way it binds the substances released from the damaged cells at the surface of the wound.

8. The legs of adult anurans do not regenerate. Regeneration may be induced after amputation, if the stump is traumatized by sticking a needle into it several times (Polezhayev). In the adult frog, regeneration following amputation may result from treatment of the wound with a hypertonic salt solution, or from the implantation of tadpole skin (Rose).

9. In mammals, the bones of the extremities are able to regenerate, but not the bones of the adult skull. In young mammals, however, the bones of the skull also are able to regenerate. Regeneration has been induced in the adult by implantation of a "sawdust" made from skull bones into the cavities of bone defects. A similar method has been employed to induce regeneration of the dentine in the teeth of dogs (Polezhayev). The brain of young mammals is able to regenerate in the presence of brain membrane and in the absence of blood clots (Polezhayev).

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ERRATUM

In the article, "Soviet Cellular Biophysics 1950–1960," by Richard B. and Jane K. Setlow, published in the March, 1961, issue of the *Quarterly Review of Biology*, p. 20, column 2, line 19, should read: "Troshin wrote a book on this subject (reviewed by Nasonov, 1959, now deceased) . . ."

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will occasionally appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to H. B. Glass, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *Department of Biology, The Johns Hopkins University, Baltimore 18, Maryland, U. S. A.*

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GENERAL BIOLOGY: PHILOSOPHY AND EDUCATION

SCIENCE AND LIBERAL EDUCATION.

By Bentley Glass. Louisiana State University Press, Baton Rouge. $3.00. xii + 115 pp. 1960.

This volume comprises the three Davis Washington Mitchell Lectures presented at Tulane University in March 1958. They combine a concise discussion of science, with emphasis on genetics, in the service of man; the significance of a liberal education in this scientific age; and a philosophical evaluation of the impact of science and education on the concepts of evolution. The author presents an historical background and lucidly summarizes progress in science and education during the past century. He then presents a resume of the "confusing flow and counterflow of argument and philosophy" dealing with conceptual developments in Darwinian evolution and human values. He maps many areas of thought, but leaves their exploration to the reader, an essential element of good pedagogy.

The essay on Genetics in the Service of Man illustrates the relation of scientific progress to man's increase in power, using genetics as the example. The application of scientific knowledge to population growth and potential food abundance is employed to emphasize man's power to direct biological and social development for incalculable good or incalculable harm. The four major genetic factors, mutation, natural selection, genetic intermixture, and chance, that are known to contribute to evolutionary change, are discussed and illustrated with examples. In turning to the "risks" and the "quandaries" involved in the use of the large volume of recently acquired basic information, the author stresses mainly the danger of doing irreparable damage to the hereditary material of man, although he does allude to the constructive application of this knowledge to human welfare in the second essay.

In developing the theme of Liberal Education in a Scientific Age, the author expresses "a few opinions, in the hope of challenging some thought on the subject." Stress is placed upon the liberal education as a means of developing the "freedom of the mind that grows out of an indomitable quest for truth." The continued increase in man's power, elucidated in the first essay, is dependent upon a transmission of knowledge from one generation to the next, extending and testing its validity and enlarging the comprehension by man of his place in the universe. "The sciences are the greatest educational forces in generating true freedom of the mind, and they must in fact constitute the heart of truly liberal education." Science as the core of the

educational process must be communicated imaginatively by systematically exploring the unknown aspects of nature, integrating experiences, and developing a workable philosophy of life. This denotes personal participation in a great social enterprise that involves science as the core and that is pervaded by beauty, order, and many unknowns. The child and young adolescent are able candidates for this experience. The subject is germane, for modern life is now permeated with science and civilization rests upon scientific foundations. A scientifically determined philosophy is essential in coping wisely with the social and political problems of the modern world. This educational process must be advanced internationally to accomplish the incalculable good. How can this be consummated?

Science by its very nature is international in pursuit, application, communication, and role in education. Languages, behavioral characteristics, philosophies, and power politics represent the major barriers. Through the cooperation of scientists, philosophers, and educators, and the universal recognition that "the whole of nature is far beyond man's present comprehension, the edifice of science and philosophy a mere foundation, and not the completed structure it will some day be," lie our hopes for the future.

The essay on Darwinian Evolution and Human Values turns specifically to the problem of the relation between human values and biological evolution. The biological, philosophical, and ethical implications of Darwinian and pre- and post-Darwinian evolution are discussed and thought-stimulating questions asked. These concepts and experimentation have "placed in man's hands the power to create new forms of life and to remold his own nature." "Science must aid him in finding, through ethics, the humility to make that power safe."

J. G. Dickson

Man and Learning in Modern Society. *Papers and Addresses Delivered at the Inauguration of Charles E. Odegaard as President of the University of Washington, November 6 and 7, 1958.*

University of Washington Press, Seattle. $5.00. x + 186 pp.; ill. 1959.

The Inauguration of Charles E. Odegaard as president of the University of Washington in November of 1958 provided the opportunity for a group of articulate scholars to take a look at the university as it carries out its function in the society of today. The lectures were organized in three blocks: Education and American Society; Physical and Biological Sciences and Technology; and The Humanities in the Modern World.

The three speakers in the first block were Clark Kerr, president of the University of California; Eugene V. Rostow, dean of the School of Law, Yale University; and Erwin D. Canham, editor of the Christian Science Monitor. Looming large in the background of all of the talks, implicit or explicit, was the menace of the Soviet system and the attention of the emerging nations of Africa and Asia to whom we would speak and who would listen. In this frame of reference it was Dean Rostow, speaking on Education for a Society of Law, who had the most to say in his discussion of the liberation of the individual for creative self-development within a civilized society, and of the function of the university in fostering this ideal. To quote Pasternak's words from *Doctor Zhivago*: "What has for centuries raised man above the beast is not the cudgel, but an inward music: the irresistible power of unarmed truth, the powerful attraction of its example."

The talks by Kerr on Education for the Scientific and Industrial Age, and by Canham on Education and the Problem of Communication were of a more diffuse character, although pertinent to their respective topics.

Polykarp Kusch, Nobel laureate of Columbia University, discussed Physical Science—Present and Future. The paper is provocative, penetrating and sensitive, a presentation by a humanist who also happens to be a physical scientist. It deals with the limitations of the science as well as its potentialities for new knowledge and new power, with the influence this knowledge and power has had on our lives and philosophical thought, and with use and misuse of knowledge to ennoble or degrade mankind. Melvin Calvin's Round Trip from Space is a more parochial treatment of the question "Whence came life on the surface of the earth?", a topic that has been variously treated by a number of scientists in the last few years.

I am less prepared to judge critically the next three papers dealing with the Humanities in the Modern World, but it seems to me terribly important in this day when science and technology are given overwhelming priority in terms of support and manpower that we listen closely to such speakers as Arthur Woodhouse, George Boas, and G. H. Forsyth who, far from being apologists, see very clearly the place of literature, philosophy, and the fine arts in the total picture of the university and its functions, and of our daily living, and who, recognizing the importance of science, understand also that the humanities are of "tremendous significance as a channel—perhaps the only channel—through which the rarefied abstractions of modern science can penetrate the world of men, can be humanized." From the point of view of the humanist, they discuss the same problem which C. P. Snow has lately dramatized, and they show an acute awareness of the problems involved in the under-

standing and the degree of respect accorded the various areas of creative endeavor; but with greater perceptiveness and totality of outlook they also offer a guiding hand rather than point the finger of doom. To quote the words of F. S. C. Northrop, via Forsyth, "What cannot be grasped by everyone literally in terms of the concepts of the scientist and scientific philosopher, can be suggested and presented analogically with vividness and moving power, by recourse to the concepts by intuition of the artist. Here the art of the future will find its message for men. Its task will be to take the new conception of the theoretic component of reality which contemporary science is now making articulate, and to convey this conception metaphorically, in terms of the vivid aesthetic materials given in immediate intuition. . . . Such is the difficulty, and by the same measure the importance, of the task of the artist of the future."

The volume is concluded by two inaugural addresses, one by President Nathan Pusey of Harvard University on The Joint Responsibility of Public and Private Universities, and the other by incoming President Odegaard. Their contents are appropriate to the occasion.

C. P. SWANSON

GENESIS AND GEOLOGY. *A Study in the Relations of Scientific Thought, Natural Theology, and Social Opinion in Great Britain, 1790–1850.*
By Charles Coulston Gillispie. Harper Torchbooks, Harper & Brothers, New York $1.75 (paper). xiv + 306 pp. 1960. (Reprint of 1951 edition.)

THE PHILOSOPHY OF SCIENCE. *An Introduction.*
By Stephen Toulmin. Harper Torchbooks, Harper & Brothers, New York. $1.25 (paper). 176 pp.; ill. 1960. (Reprint of 1953 edition.)

MAN'S PLACE IN NATURE.
By Thomas H. Huxley; introduction by Ashley Montagu. The University of Michigan Press, Ann Arbor. $1.75 (paper). iv + 184 pp.; ill. 1959. (First published in 1863.)

YOU AND THE UNIVERSE.
By N. J. Berrill. Fawcett Publications, Greenwich, Conn. Fifty cents (paper). 175 pp. 1959. (Reprint of 1958 edition.)

OF SOCIETIES AND MEN.
By Caryl P. Haskins. The Viking Press, New York. $1.45 (paper). xiv + 282 pp. 1951. (Reprint of 1951 edition.)

DOUBT AND CERTAINTY IN SCIENCE. *A Biologist's Reflections on the Brain.*
By J. Z. Young. Oxford University Press, New York. $1.50 (paper). xii + 168 pp.; ill. 1960. (Reprint of 1951 edition. New 3-page preface.)

STUDIES IN HUMAN TIME.
By Georges Poulet; translated by Elliott Coleman. Harper Torchbooks, Harper & Brothers, New York. $1.75. xii + 363 pp. 1959. (Reprint of 1956 edition.)

GENERAL BIOLOGY.
By Morris Winokur; illustrated by Herbert Ruckes. Littlefield, Adams & Co., Paterson. $1.50 (paper). xvi + 267 pp.; ill. 1960.
This volume of the Littlefield College Outlines series purports to be "a condensed textbook, not a bare and fragmentary outline." It is true that the book does not assume the outline form common in such booklets, but it is certainly bare and fragmentary enough. It reflects the opinion of the author that "general biology" consists principally of a parade of the plant and animal kingdoms, plus a section on human anatomy and physiology. There are also shorter sections on heredity and evolution. Throughout the booklet the emphasis is on anatomical detail, and the student is admonished to memorize the glossary definitions if he wants to do well on his examinations. There is little in this booklet to distinguish its subject matter from the usual high school biology course of yesteryear, unless it is the burden of technical terminology and the void of general principles and concepts. The book is described as an "up-to-date exposition," but evolution stops with T. H. Huxley, mitochondria are nowhere mentioned, and of course, not a word about ATP or DNA can be found. By some oversight, one chemical equation did get into the text: the "summary equation" of photosynthesis.

FRANK C. ERK

BIOLOGY: HISTORY AND BIOGRAPHY

SOURCE BOOK OF MEDICAL HISTORY.
Compiled with notes by Logan Clendening. Dover Publications, New York; Henry Schuman, New York. $2.75 (paper). xvi + 685 pp. 1960. (Reprint of 1942 edition.)

THE LIFE OF PASTEUR.
By René Vallery-Radot; translated from the French by Mrs. R. L. Devonshire. Dover Publications, New York. $2.00 (paper). xxiv + 484 pp. 1960. (Reprint of 1906 edition.)

SCIENCE SINCE 1500. *A Short History of Mathematics, Physics, Chemistry, Biology.*
By H. T. Pledge. Harper Torchbooks, Harper & Brothers, New York. $1.85. (paper). 357 pp. + 15 pl.; text ill. 1960. (New 2-page preface. Reprint of first (1939) edition.)

A History of Science, Technology and Philosophy in the 16th & 17th Centuries. *Volume II.*

By A. Wolf with cooperation of F. Dannemann and A. Armitage. Harper Torchbooks, Harper & Brothers, New York. $1.95 (paper). xvi + pp. 350–686; ill. 1959. (Reprint of second (1950) edition.)

THE YOUNG NATURALIST

Science Survey.

Edited by A. W. Haslett and John St John. The Macmillan Company, New York. $5.75. 360 pp.; ill. 1960.

The British Association for the Advancement of Science has cooperated with the publishers in the preparation of this book for the general public, and has succeeded in getting together a group of authors of distinction to discuss their own topics of science in language generally stripped of obscure jargon. The chapters are grouped under the following major headings: The tuff of the universe; Arranging atoms for industry; Cells, viruses and heredity; Radiation and fall-out; Organisms and their behavior; The earth; and Space exploration.

The biologist will find the following chapters of immediate interest; Cells and their reproduction (T. S. Work); Bacterial cell walls (J. Baddiley); Building viruses (Sidney Brenner); Haemoglobin and its variations (V. M. Ingram); Genetics and "The Origin of Species" (J. Heslop-Harrison); Evolution of courtship behaviour (A. Manning and M. Bastock); Modern views of fish migration (P. A. Orkin); and Time to react (D. E. Broadbent). Each is excellently written and illustrated, and each gives a broad picture of the problems making these areas of study worth the time and thought of intelligent men.

No less interesting are the 8 chapters dealing with the earth and with space, for they convey to the reader something of the reasoning and excitement which lie behind enormously expensive projects such as the mohole and satellite orbiting.

Sir George Thomson, FRS, in a Foreword, points out that the BAAS, like our own AAAS, is becoming more and more an organization for the popularization of science at all levels, and justifiably so, since science provides not only the basis for technological advancement but also the new ideas which gradually but powerfully shape our culture and our future directions. Those who occupy responsible positions must know of these things if they are to guide wisely the society in which we live and have our being.

C. P. Swanson

Ten Little Housemates.

By Karl von Frisch. Pergamon Press, New York, Oxford, London, and Paris. $3.00. 146 pp.; ill. 1960.

This is a charming little book designed to introduce the average householder to the common insects and their relatives who share his house. It is written with sympathy and understanding toward the wee beasties. Unobtrusively scattered among the fascinating and frequently humorous paragraphs are numerous bits of basic scientific information. One may read this book purely for enjoyment and come away a more soundly educated entomologist.

Utterly delightful.

Vincent G. Dethier

Viruses and the Nature of Life.

By Wendell M. Stanley and Evans G. Valens. E. P. Dutton & Co., New York. $4.95. 224 pp.; ill. 1961.

The development of a new era in useful communication between men is advanced by the appearance of this creatively illustrated and authoritative book. Appreciation of the book and its contents does not require the viewing of the companions in this educational endeavor: eight half-hour films designed for television presentation. The book is written by W. M. Stanley and six other outstanding research scientists, in collaboration with E. G. Valens, no newcomer to the field of comprehensive yet nontechnical science writing for youth. The result of this collaboration is an intriguing presentation to the intelligent high school student or layman of one area of biology. It is largely a story of viruses and their components, nucleic acids and proteins, as they are now pictured in the present state of our knowledge. Comfortably woven into the story are some insights into the development of these current concepts, techniques used in their elucidation, and anticipation of continued dynamic developments in biological research. No previous knowledge of the maze of intricate terminology and jargon which abounds in the scientific disciplines of chemistry, genetics, and virology is required. The excellent photographs and text stress elementary concepts—they introduce only essential and basic scientific terminology on a schematically presented framework that is readily followed. There are a few gaps in this progression. Most of these are occasioned by the lack of legends and titles for most of the illustrations, a deficit not always entirely compensated for by adequate description in the text.

Philip E. Hartman

Adventuring with Beebe. *Selections from the Writings of William Beebe.*

By William Beebe. The Viking Press, New York. $1.25 (paper). 282 pp.; ill. 1960. (Reprint of 1955 edition.)

A Book About Bees.

By Edwin Way Teale. Indiana University Press, Bloomington. $1.95 (paper). 208 pp.; ill. 1959. (Reprint of 1940 edition: *The Golden Throng.*)

ECOLOGY AND NATURAL HISTORY

Djuren i. Färg. *Däggdjur-Kräldjur-Groddjur. Text AV.*

By Kai Curry-Lindahl. Almquist & Wiksell, Stockholm. 190 pp. + 109 pl. 1960.

This is another in the series of pocket-size books in color by Curry-Lindahl, this one depicting the mammals (Däggdjur), reptiles (Kräldjur), and amphibians (Groddjur) of Sweden. There are 109 colored plates done by the naturalist-artist, K. A. Tinggaard, and the text, which is in Swedish, includes information on systematics as well as general class and species descriptions. The book will be found useful because of the plates, but an understanding of the text will be limited to those few outside of Scandinavia who have a command of the Swedish language.

C. P. Swanson

Audubon and His Journals. *Vols. I and II.*

By Maria R. Audubon with zoological and other notes by Elliott Coues. Dover Publications, New York. $2.00 (per volume). (Vol. I) xiv + 532 pp.; ill.; (Vol. II) viii + 554 pp.; ill. 1960. (Reprint of 1879 edition.)

Zoogeography of the Swedish Amphibians and Reptiles. *With Notes on Their Growth and Ecology. Acta Vertebratica, Vol. I, No. 3.*

By Torsten Gislén and Hans Kauri. Zoological Department of Nordiska Museet and Skansen, Stockholm. 40 Swed. Crowns (paper). viii + pp. 199–397; ill. 1959.

The task of writing this book had occupied Gislén for a long period of years, and at the time of his death, in 1954, the manuscript was almost completed. It was revised by Kauri, himself a well-known specialist in amphibians, who added considerably from his own experience.

The Swedish fauna is poor, containing no more that 18 indigenous species of the groups treated: 12 amphibians (including 2 newts) and 6 reptiles (3 lizards, 3 snakes). The distribution in Sweden is recorded on detailed dot-maps, which seem to provide satisfactory information for all species, except perhaps for *Rana arvalis* in the north, long confused with *R. temporaria*. Besides these two, the following species proceed to the north of the Polar Circle: *Triturus cristatus, Bufo bufo, Lacerta vivipara, Natrix natrix,* and *Vipera berus.* The reptiles going farthest north (*L. vivipara* and *V. berus*) are both viviparous.

Great attention is paid to infraspecific variability. The most interesting case is that of *Triturus vulgaris,* which in the northern part of its area (62–65° N) constitutes a morphologically well-defined population, described by Kauri as subsp. *borealis.* It shows a tendency to be neotenous.

The development cycles, notably as dependent on climate and other biological features, are described in detail, as are the breeding places of the amphibians.

Carl H. Lindroth

EVOLUTION

The Theory of Evolution.

By J. Maynard Smith. Penguin Books, Harmondsworth, Middlesex. 85 cents (paper). 320 pp.; ill. 1960.

This volume is the first of the new Pelican Biology series. The main purpose of this new series, according to the editorial Foreword, is to acquaint the layman with the *ideas* of modern biology. It is significant that the first idea to be so broached is perhaps the principal one that characterizes modern biology, the idea of evolution—not that the idea itself is new, but surely its pervasive role in every area of the contemporary biological scene deserves special attention.

John Maynard Smith's efforts in behalf of the theory of evolution are to be applauded. To write such a book without the assistance of a great deal of genetics, paleontology, embryology, and ecology is probably impossible, if the book is to be meaningful at all, and Smith does not attempt to do it. But the observational and experimental support for the theoretical structure is so unobtrusively provided that one never loses the essential thread of the argument. Even for the rare person who has never heard of genetics, if indeed he exists any longer, the requisite information is efficiently and interestingly presented in a special chapter.

The heart of the book comes in four chapters dealing with species—their nature, their origins, the mechanisms of isolation, and finally the genetics of species differences. Two chapters each on the patterns of evolution and on the origins of the major groups are excellently conceived. The author has appended suggestions for further reading, a glossary, a bibliography for each chapter, and an index. The most distressing thing about the book is that its cost was $0.85 when it was received for re-

view, but when I next passed the bookseller's rack, the same pages had donned a new tricolor cover, and the price had evolved in one macromutational step to $1.95.

FRANK C. ERK

PRINCIPLES OF PALEOBOTANY. *Second Edition.*
By William C. Darrah. The Ronald Press Company, New York. $6.50. x + 295 pp.; ill. 1960.

This is a revised edition of a book published in 1939. The 1939 text represented an important contribution to American paleobotanical literature because morphological paleobotany had just become firmly established in this country and it was possible to depart from the almost exclusive use of European illustrative material. A serious drawback of that volume was the scarcity of figures.

The revised book remedies this situation to some extent. There are many more illustrations than in the first edition—most of them ink drawings. What halftone reproductions are included are also primarily of drawings, mostly of reconstructed plant groups. It is unfortunate, however, that no photographs of actual plant fossils were used. Furthermore, the quality of illustrations ranges from excellence to crudity.

Although this work is a fairly recent publication, and the author in his preface states that "many developments in paleobotany since 1939 have materially altered major points of view" and "attempts have been made to summarize these newer discoveries and to suggest their implications," the book has not really been brought up to date. It is surprising how few references are made to papers published in 1950 and after. Ten years ago this volume would have been an exceptional one; at the present, it is just another text with limited use.

In its defense, one must agree that the material is interestingly presented, attractively assembled and printed, and comprehensive in topics covered. Its greatest value would probably be on the shelf of a non-paleobotanist wishing a general, but not detailed, reference book on fossil plants.

THEODORE DELEVORYAS

STUDIES IN PALEOBOTANY.
By Henry N. Andrews, Jr.; chapter on palynology by Charles J. Felix. John Wiley & Sons, New York and London. $11.75. x + 487 pp.; ill. 1961.

The field of paleobotany is far from a static one. New discoveries continue to come to light; new ideas concerning plant evolution in past ages are presented; reports of plant remains in older and older deposits are made known. This text does an admirable job in summarizing most of our present paleobotanical knowledge. It is not intended as a comprehensive reference volume but is, rather, a text in which a fortunate choice of material has been selected. In this up-to-date treatise the historical aspects of the field are not neglected. This kind of treatment has appeal to students who generally appreciate some of the humanistic aspects of a science.

Andrews departs from the usual arrangement of topics. Because his underlying theme is plant evolution, many of the chapters are arranged to reflect his ideas concerning phylogenetic relationships. His early chapters are placed in a sequence leading from psilophytic forms, through ferns and seed ferns, to the angiosperms. Although far from settled, such a suggested line of evolution leading to the flowering plants is at least as good as any other scheme offered. Arrangement of some of the subsequent chapters reflects his views on a possible polyphylesis in the vascular plants.

One of the attractive aspects of this new text is the personal tone of the writing. This does not mean that the book lacks in objectivity; indeed, the author, in spite of introducing many of his own interpretations, indicates more than one way to view certain problems and is far from dogmatic. Such a personal style would be out of place in a comprehensive reference book, but it makes a student's textbook considerably more attractive. The reviewer can attest to this because he has already used the book for a one-semester course in which it had an excellent reception by the students.

A text in this field would be almost useless without copious illustrative material. *Studies in Paleobotany* has an abundance of illustrations of excellent quality. Photographs are clear and line drawings sharp and most of them expertly executed. A few pictures, unfortunately, have suffered slightly in the reproduction.

One hopes that the author agrees to keep this valuable textbook usable for many years to come with a series of revised editions which will keep up with still newer discoveries.

THEODORE DELEVORYAS

LEHRBUCH DER PALÄOZOOLOGIE. *Band II. Invertebraten. Teil 2. Mollusca 2—Arthropoda 1.*
By Arno Hermann Müller. Veb. Gustav Fischer, Jena. DM 66.— xii + 448 pp.; ill. 1960.

This is the third volume to appear of a projected five-volume work on fossil animals by Müller, of the Bergakademie, at Freiberg, East Germany. The new volume covers Gastropoda, Cephalopoda, Merostomata, Arachnida, Pycnogonida, and Trilobitomorpha.

The first volume of the series (*Q.R.B.*, 33: 68. 1958), published in 1957, was devoted to general ma-

terial, especially the basic principles of paleontology, a subject to which Müller had previously made many original contributions. The second, covering Protozoa, Archaeocyatha, Porifera, Coelenterata, Bryozoa, Brachiopoda, "Vermes", and part of Mollusca (Amphineura, Scaphopoda and Lamellibranchiata), appeared in 1958. The two remaining volumes are scheduled to appear in 1961 and 1962. They will include the higher arthropods and echinoderms, and the vertebrates.

The *Lehrbuch*, written in the great tradition of Zittel's *Handbuch der Paläontologie*, somewhat resembles the French *Traité de Paléontologie* in scope, but is not as comprehensive in coverage of invertebrates as the international *Treatise on Invertebrate Paleontology*. Müller's important work may be too large for wide adoption in university courses, but it will provide a most useful and convenient summary of paleontological theory and principles, particularly as developed by the German school of paleontology. It contains innumerable apt illustrations, many of them new, many tables and bibliographic references.

A few decades ago, university teachers of paleontology were following a taxonomic approach to the subject, and textbooks were mainly inadequate and outdated catalogues of knowledge over morphology, classification, and distribution in time and space of genera of fossil organisms. The rapid accumulation of factual knowledge soon caused a shift in emphasis away from factual details to general interpretations illustrated by selected examples.

Müller's *Lehrbuch* is an admirable compromise between more or less superficial generalities imposed by the limitations of a single volume and the more desirable, but expensive and nearly unattainable encyclopedic coverage of the fossil records of the vast number of animal groups. It contains descriptions and illustrations of a large number of the better known genera of fossil animals, but inevitably it is not adequate for, and was not intended to serve as a basis for, identification and classification of varied fossil faunas.

NORMAN D. NEWELL

ASPECTS OF THE ORIGIN OF LIFE.
Edited by M. Florkin. Pergamon Press, Oxford, London, New York, and Paris. $5.00. viii + 199 pp.; ill. 1960.

The present book is a series of articles selected from the *Proceedings of the Symposium on the Origin of Life on the Earth*, held in Moscow under the sponsorship of the USSR Academy of Sciences. These facts seem particularly appropriate since it has been the Russians, and especially A. I. Oparin, who gave first voice to our current ideas of spontaneous generation and who have stimulated research which may ultimately aid us in understanding the early beginnings of life on earth. The papers were selected with a view to conveying to the layman and to scientists in other fields what is going on in this area. As such, they provide understandable and readable discussions of the primeval state of the earth and its atmosphere, the development of the biosphere, the first-formed organic complexes and their possible methods of genesis, the origin of duplicating systems, and the origins of life forms. A number of Russian scientists present intriguing speculations, as do J. D. Bernal, S. L. Miller, S. W. Fox, N. W. Pirie, M. Calvin, H. C. Urey, L. Pauling, and R. L. M. Synge. The layman who picks up this book will find the going rather difficult, for a goodly amount of biochemical knowledge is taken for granted by some of the authors; the reader who surmounts these problems, however, will find much of interest and stimulation in the various chapters.

C. P. SWANSON

NATURAL SELECTION AND HEREDITY.
By P. M. Sheppard. Harper Torchbooks, Harper & Brothers, New York. $1.35 (paper). 209 pp.; ill. 1960. (Reprint of 1959 edition.)

THE MECHANISM OF EVOLUTION.
By W. H. Dowdeswell. Harper Torchbooks, Harper & Brothers, New York. Ninety-five cents (paper). x + 155 pp.; ill. 1960. (Reprint of second (1958) edition.)

GIANTS OF GEOLOGY.
By Carroll Lane Fenton and Mildred Adams Fenton. Dolphin Books, Doubleday & Company, New York. Ninety-five cents (paper). 318 pp.; ill. 1960. (Reprint of 1952 edition.)

THE ORIGIN OF SPECIES *by Means of Natural Selection; or the Preservation of Favored Races in the Struggle for Life.*
By Charles Darwin. Dolphin Books, Doubleday & Company, Garden City. Ninety-five cents (paper). 517 pp. 1961.

This is but one of the many reprints of Darwin's works that have appeared from time to time. What else can one say? The cost is low, the print is legible, and the substance is as pertinent as it ever was.

C. P. SWANSON

GENETICS AND CYTOLOGY

THE ORGANIZATION OF CELLS *and Other Organisms.*
By Laurence Picken. Oxford University Press, New York and London. $13.45. xxxviii + 629 pp. + 34 pl.; text ill. 1960.

The author of this scholarly work has set himself

the task of showing that it is feasible, indeed proper, to consider bacteria, viruses, and the multicellular organisms (plant and animal) under one cover, and that they are all fit objects for the cytologist's efforts. This is accomplished by dealing with the organisms in terms of their organization—neither structure nor function specifically, but, as he puts it, the "integration of activities in time." He holds no brief for structure versus function—it is a meaningless dichotomy—but concerns himself with attempting to understand how the system operates as determined by what the cytologist's tools (very broadly defined) can reveal.

The 10 chapters reveal his pattern of analysis: The Organization of Cells and Other Organisms; The Organization of Viruses; The Organization of Certain Schizomycetes; The Organization of Cells (The Nucleus); The Organization of Cells (The Cytoplasm—Bulk Properties); The Organization of Cells (The Cytoplasm—Cytoplasmic Particulates and Membrane-systems); The Organization of Cells (The Cytoplasm—Fibrillar Cytoplasmic Structure); The Organization of Cells (The Cell Surface and Cell Membranes); Extracellular Materials and Structures and Their Role in the Spatial Extension of Cellular Activities; Becoming Multicellular as Seen in the Light of Cell Properties; and an excellent and interesting Envoi. We are thus not surprised to find a discussion of pyrenoids, chromosome movements, amoeboid motion, chitin, active transport, collagen, and many more, since the author's goal is to show how organization in space and time is the determinant parameter in defining his taxonomy.

Although Picken terms this a work of compilation, it is clearly more than this. It is an expression of his belief of what constitutes the cytologist's bailiwick. The 7 pages of the Table of Contents (remarkably analytical) attest to this, as do the 70 pages of bibliography, comprising an excellent reference list. It is not surprising in a monograph of this magnitude to find that the bibliography is not uniformly up to date.

Unfortunately, though the author's excellent philosophical observations pervade the book, interest is not maintained throughout. The amount of detail is enormous; few readers will find it all equally interesting, but there are many things herein for all biologists.

Picken has admirably accomplished his goals of compilation and documentation of his viewpoint. These goals, with his opinions and philosophy, justify his efforts, for the volume should indeed broaden the view of cytology and cytologists.

WILLIAM J. YOUNG

EXPLORATIONS INTO THE NATURE OF THE LIVING CELL.
By Robert Chambers and Edward L. Chambers. Harvard University Press, Cambridge. $8.00. xxiv + 352 pp.; ill. 1961.

This is a highly personal book, in that it brings together those aspects of cytology which were of paramount interest to Robert Chambers during a long lifetime of active experimentation. Being personal, a certain amount of bias is inevitable, but this is mainly in terms of content rather than of interpretation. Robert Chambers died in 1957, but his son, Edward L. Chambers, has carried the book through to publication.

Robert Chambers was a micromanipulator in so far as techniques are concerned, but his focus was always on the physical and chemical aspects of living cells. These he approached by employing the tools of microdissection and microinjection, with the results embodied in several hundred research papers. After an initial statement relating to the unity of the cell as an integrated mass of protoplasm, the book deals principally with the extraneous coats of the cell, the plasma membrane, or protoplasmic surface film as it is here referred to, the action of various salts on protoplasm, the hydrogen ion concentration of cell components, the penetration of dyes and the problem of vital staining, the components and processes of cell division, and a final section on the micromanipulative method. An appendix deals with the techniques of micromanipulation and with procedures for the determination of intracellular pH by microinjection. The bibliography contains a listing of all of Robert Chambers' papers and a general bibliography of papers relating to those topics which were of interest to him.

Omitted from consideration are such areas of current research as the fine structure of cellular components as revealed by electron microscopy, labelling studies with radioactive isotopes, and nuclear cytology in many of its ramifications. It would have been well to have had Chambers' integration of these results with those from his own investigations. Even so, the book covers a great deal of ground not ordinarily found in the conventional cytology text, and as such is a monument to an indefatigable student of the cell.

C. P. SWANSON

THE CELL. *Biochemistry, Physiology, Morphology. Volume IV. Specialized Cells: Pt. 1.*
Edited by Jean Brachet and Alfred E. Mirsky. Academic Press, New York and London. $18.00. xvi + 511 pp.; ill. 1960.

THE CELL. *Biochemistry, Physiology, Morphology. Volume V. Specialized Cells: Pt. 2.*
Edited by Jean Brachet and Alfred E. Mirsky. Academic Press, New York and London. $20.00. xvi + 597 pp. + 7 pl.; text ill. 1961.

It is a pleasure to see these volumes make their appearance, and to note that they are up to the quality

of writing and substance set by the authors of Volume I (*Q.R.B.*, 35: 146. 1960). It is to be hoped that Volumes II and III will follow soon since these are central, as regards topics, to the heart of cellular biology. The two present volumes are more specialized in nature and deal in particular with cellular types that have been widely used in a variety of biological studies.

It is not possible to review each chapter in detail here, but a general knowledge of content can be gained by a listing of chapter headings, while the competence of each review can be judged by the fact that each author is an outstanding authority in his or her field. The contents of Volume IV are: Viruses (R. Thomas); Outline of the visible organization of bacteria (C. F. Robinow); Protozoa (D. L. Nanney and Maria A. Rudzinska); Intracellular parasitism and symbiosis (W. Trager); The Neuron (H. Hydén); Visual photoreceptor structures (W. H. Miller); and Muscle cells (H. E. Huxley). Volume V includes: Gland cells (M. Gabe and L. Arvy); Kidney cells (R. P. Forster); The blood cells and their formation (M. Bessis); Bone and cartilage (P. Lacroix); Skin and integument and pigment cells (W. Montagna); Antibody formation (P. D. McMaster); The morphology of the cancer cells (Ch. Oberling and W. Bernhard); and Biochemistry and physiology of the cancer cell (Eliane Le Breton and Yvonne Moulé).

The two volumes are, of course, reference texts; as such they are well documented, the paper is of high quality and very legible, and the illustrations are exceptionally good. The cytologist who must keep himself abreast of what is going on can hardly afford to be without access to them, although the price makes them more likely candidates for the library shelf than for the cytologist's personal office.

C. P. SWANSON

INTERNATIONAL REVIEW OF CYTOLOGY. *Volume X. Prepared Under the Auspices of The International Society for Cell Biology.*

Edited by G. H. Bourne and J. F. Danielli. Academic Press, New York and London. $13.00. xiv + 409 pp.; ill. 1961.

The first article in this volume deals with the chemistry of the Schiff reagent, an important dye stuff used in cytology and in cytochemistry whose affinity for aldehydes has been the basis of a good deal of qualitative and quantitative work. Its affinity and specificity for DNA has proven to be of great usefulness, but since the chemistry of the reactions is still imperfectly known, the question of using the reagent in the plasmal reaction for the certain identification of cytoplasmic molecules remains open. It is clear that much remains to be done in this particular area.

A. K. Sharma and A. Sharma are the authors of the next article, on spontaneous and chemically induced chromosome breaks. Other than being a good source of literature bearing on this subject, the presentation is a badly muddled one with a number of conclusions supported by tenuous and often irrelevant data. It is not a sound contribution to a rather complex and perplexing field.

Somewhat the same judgment can be made of the third paper, by S. Wischnitzer, which deals with the ultrastructure of the nucleus and nucleocytoplasmic relations. Admittedly there are many observations via electron microscopy of the nucleus and its cytoplasmic boundary, and the gap between the EM image of a chromosome and that drawn from visual and isotopic studies is a very large one, but the need is not for another recitation of these but rather for an attempt to fit the information into a more meaningful picture of nuclear architecture. I have no feeling that this has been done.

L. Wolpert's discussion of the mechanics and mechanism of cleavage is an attempt, and a successful one, to deal with a rather difficult problem. After a review of the literature and of existing theories, he presents his own theory of astral relaxation which seems to account for most of the observations that have been made. The theory considers that there is a uniform tension over the surface of an egg prior to cleavage, that the asters cause the polar regions to differentiate, and that this differentiation leads to a surface relaxation which then permits the cleavage furrow to develop in those areas where the tension is still high. The problem still remains to be discussed in chemical and molecular terms.

The remaining articles deal with the following topics: Growth of the liver with special reference to mammals (F. Doljanski); Cytological studies on the affinity of the carcinogenic azo dyes for cytoplasmic components (Y. Nagatani); and Epidermal cells in culture (A. G. Matoltsy). All are readable and competently done, and keep strictly within the narrow confines of their subjects.

C. P. SWANSON

THE CELL NUCLEUS. *Proceedings of an Informal Meeting Held at the Department of Radiotherapeutics, University of Cambridge, 31 Aug.–1 Sept., 1959, by The Faraday Society.*

Chairman: J. S. Mitchell. Academic Press, New York; Butterworths, London, Toronto, Sydney, Wellington, and Durban. $11.00. xiv + 269 pp.; ill. 1960.

It is significant that the Faraday Society should turn its attention, and give its support, to a meeting dealing with the nuclei of cells. This is recognition of the fact that an understanding of the physical and chemical architecture and machinery of the nucleus requires the collaboration of workers from a number of disciplines, and that biology today is worthy of the attention of the physicist, chemist, and math-

ematician as well as of the traditional botanist, zoologist, and biochemist. A goodly portion of the papers presented at the symposium are consequently of a physical and chemical nature, and fall into 5 major groupings: function of the nucleolus; synthesis of DNA from small molecules; synthesis of DNA in the cell; nuclear enzymes; and the structure of DNA-protein in solution and in the nucleus.

The volume consists of 38 papers, together with the appropriate discussions relating to each of the contributions. The authors, internationally representative, are among our most active and thoughtful investigators, so the volume as a whole represents an up-to-date summary of the molecular architecture and biochemistry of the nucleus, including speculations, controversies, and new avenues of approach. As such, it is a "must" volume for the cell biologist who would keep up with this rapidly moving field. Mitchell and his colleagues are therefore to be congratulated not only for the organization of the symposium but also for the recognition of the pertinence of the topics and the rapid publication of the papers.

C. P. SWANSON

AN INTRODUCTION TO MEDICAL GENETICS.
By J. A. Fraser Roberts. Oxford University Press, London, New York, and Toronto. $7.00. xii + 259 pp.; ill. 1959.

Fraser Roberts' book is probably, as he indicates in the preface, unique (in the English language) in its presentation of medical genetics exclusively in terms of man and human disease. Examples from other forms of life are excluded. The treatment is made as nonmathematical as possible. Lamy of Paris has prepared a comparable text in French.

The author should be given a hearty vote of thanks for providing an answer to the frequently recurring question from clinicians and medical students with lukewarm interest, "Where can I read up on medical genetics?" The book is not, and is not intended to be, suitable as more than an introduction for the serious student of human heredity.

Still there is much that the serious student will learn from this master at the teaching, research, and clinical practice of medical genetics. The choice of illustrative pedigrees for various modes of inheritance is, in many instances, interesting. One form of keratosis follicularis is presented as an example of a sex-linked dominant or intermediate characteristic (p. 99). The pedigree of microphthalmia is an interesting example of sex-linked recessive inheritance (Fig. 45); the affected males do not live to reproduce. Komai's pedigree of cataract (Fig. 18) is an interesting possible example of the homozygous state of a "dominant" gene. The author makes the following three-way division of hereditary traits (which although distinctly arbitrary may be a useful way to think about genetic disease): (1) major harmful (and usually relatively rare) genes; (2) polymorphic traits, mostly "normal;" and (3) polygenic, or multifactorial, traits. The recent cytogenetic information on the Turner and Klinefelter syndromes and on sex determination in man is included as an addendum, but the new information on Mongolism is not included. The blood groups are particularly well discussed, and properly so in a textbook intended for general medical consumption. The author points out (p. 124) that progress with reference to the Kell blood group system is rather typical. In 1946 an antiserum was discovered which reacted positively with roughly 10 per cent of randomly selected blood (Kell-positive). Three years later a new antiserum was discovered and given the name "Cellano" for the woman who developed it as a result of fetal maternal incompatibility. The Cellano gene was found to be allelomorphic with respect to the Kell gene. Both alleles determine the presence of an antigen capable of producing a corresponding antibody. There is, therefore, no dominant-recessive relationship as might have been claimed before Cellano was identified. In discussing the genetics of common disorders, the author makes the useful point that in any large diagnostic category one can pick out one or more instances of single major gene determination. The examples cited are (1) in cancer of the colon, familial polyposis; (2) in cancer of the esophagus, tylosis; and (3) sinus infection in a striking family reported by Grunеberg. Such families, when included in large series collected for estimates of empirical risk, exaggerate the risk for the entire group; on the other hand, the risk calculated from the whole series is too low for these unusual families.

One can find fault with a few details: (1) Pieter's pedigree of alkaptonuria (*Presse méd.*, 1925), which suggests dominant inheritance, is included as a prime example of this mode of inheritance, despite the penetrating analysis of Eugene Knox (1958) which concludes that marriage of homozygotes with heterozygotes through consanguinity and isolation could account for the minority of pedigrees showing this pattern. (The recent work of Milch restudying the same kindred makes Knox's conclusion very likely.) (2) As an example of mutation, Keeler's piebald Negro family (1933), descendant from a woman born in Louisiana in 1853, is cited. The woman was the only affected child out of 9 offspring from putative parents who were normal. The probability of illegitimacy in this situation is much greater than the probability of mutation. (3) The author states, "At present, therefore, it is not necessary to assume that there is more than one gene for

elliptocytosis" (p. 147). Most interpret the linkage data as indicative of two types—one linked to Rh genes and one not linked (Lawler and Renwick). (4) In connection with gargoylism the author states, "It is believed to be essentially a disorder of lipoid metabolism" (p. 175). Although many still hold this "belief," the better recent evidence on the nature of the basic defect should have been cited. (5) It is stated, "Ordinary major genes are confined to the euchromatin. Polygenes occur in the heterochromatin, though they may occur in the euchromatin as well" (p. 201). There is some evidence to suggest that this statement is correct (see Kenneth Mather's *Biometrical Genetics: The Study of Continuous Variation*, 1949, pp. 19–22) (*Q.R.B.*, 24: 357. 1949). Information is so limited, however, that it would seem best to have avoided any mention of the view in this elementary text.

VICTOR A. MCKUSICK

CELL PHYSIOLOGY OF NEOPLASIA. *A Collection of Papers Presented at the Fourteenth Annual Symposium on Fundamental Cancer Research, 1960.*

Introduction by R. Lee Clark, Jr. University of Texas Press, Austin; for The University of Texas M. D. Anderson Hospital and Tumor Institute. $10.50. viii + 653 pp.; ill. 1960.

This volume, fourth in a series of monographs, consists of the papers presented at the cancer research symposium held in Houston in 1960. The group responsible for the planning and editing are to be congratulated for the speed with which publication has been achieved, and doubly congratulated for the excellence of the speakers and their written presentations. If there is any criticism to be made it is that, given the frequency of symposia on cellular and neoplastic topics, a certain repetitiousness is inevitable: like fashion designers, some of the participants have shifted their verbal hem, waist, and neck lines, but lacking new ideas, inspirations, and materials to catch the eye and intrigue the mind, let it become evident that last year's models have been made over. What seems to be needed in the biological world is a scientific Dior.

The symposium has been broken up into 4 major sections. The first, bearing the general title of The Nucleus, consists of 4 papers. P. C. Koller discusses the Boverian thesis that the primary cause of malignancy is abnormal chromosomal constitution, and concludes, as one might have expected, that the thesis is now untenable, that chromosomal polymorphism is variable in tumor strains and clones, and that no well-characterized neoplastic cell possesses a stable and exclusive chromosomal pattern. The Philadelphia X-chromosome, known to be associated with a particular type of leukemia, is an exception to the more general situation. G. Yerganian and his colleagues present the next paper, which deals with sex chromosomes and their relation to malignancy, transplantability, and aberrant sex determination. Most of the data have been derived from studies of the Chinese hamster, and much of the discussion concerns itself with the senior author's triheterosomic scheme of sex-determination. At best it is a confusing paper; even after three readings I am uncertain of the factual basis of what Yerganian is dealing with and to what extent his generalizations have validity, and this despite the fact that the hamster material seems to be ideal experimentally. M. J. Kopac's paper is a technical one, concerning itself with the micromanipulation of malignant nucleoli within and between cells and nuclei. The major conclusion seems to be that they are manipulable in this way. The paper by M. L. Watson is a well-organized review of current thinking on the fine structure of the nuclear envelope, and its relation to other membranous systems within the cell.

The second segment of the symposium deals with the cytoplasm. As is customary, A. J. Dalton deals in competent fashion with the Golgi complex, and concludes, with some justification, that the complex should be considered as belonging in the same category as do the mitochondria and as a regularly occurring feature of the cytoplasm of the cell. L. Dmochowski and his colleagues then discuss the morphology of tumor cells having a viral origin. Clearly this is an investigative area of much importance, and while conclusions cannot be drawn with certainty, encouraging progress is being made. A. B. Novikoff's discussion deals with the localization of enzymes in tumor cells, and in particular with that in the cells of an ascites hepatoma. Again it is evident that such cells do not depart from normality in any sharply exclusive way, although the fact that there is a shift in fine structure would suggest an accompanying shift in its biochemistry. The shift, however, may well be in regulative balance rather than in a new and distinctive pattern of enzyme activity, in which case it would be more difficult to pin down. In the last paper in this section, T. Caspersson has concentrated his interest and technical competence on the nucleolar relations in normal and malignant cells, and there remains little doubt that neoplastic cells have larger and more variable nucleoli than do their normal counterparts, and that the dry weight of the nucleoli is greatly reduced. Precisely what these data mean in terms of nuclear-cytoplasmic interactions is not yet clear, and probably will remain obscure until the significance of the nucleolus in the economy of the cell is fully clarified.

The third segment of the symposium is concerned with the nucleic acids of normal in contrast with neoplastic cells. The Leuchtenbergers (C. and

R.) have studied the DNA values of a wide variety of cells, and conclude that in normal somatic cells the DNA value is constant and double that of sperm cells; that the interphase nuclei of dividing cells, whether normal or neoplastic, have DNA values which are increased in accordance with the division process or the formation of polyploid or polytene conditions; and that infection of cells with an RNA virus does not affect the DNA values while comparable infection with a DNA virus leads to abnormally high DNA content. The reason for the latter observation still remains to be determined, particularly since it is difficult to differentiate between the cellular and the viral DNA. S. Kit has concerned himself with the structure, composition, and metabolism of tumor RNA as they are consistent with current hypotheses of the function of RNA. Little that is relatively new is added, but the review is informative, dispassionate, and ably handled. The next article, by W. S. Beck, discusses the possible relationships between malignancy and the biochemistry of RNA and its precursor molecules, a difficult problem at best but one thoughtfully treated, in that pertinent questions are raised and possible avenues of approach pointed out. The last paper in this section is by J. S. Colter and K. A. O. Ellem, who discuss the biological (infectious) activity of RNA derived from a number of RNA viruses of mammalian origin. That relatively pure RNA is infectious is clear; questions are raised, however, as to the factors promoting or inhibiting such infectivity, and the concentration of RNA, the temperature, and the presence or absence of ribonuclease are implicated without the definitive answer being provided.

Interspersed between sections of the symposium is the Bertner Foundation Lecture, The Lives of Cancer Cells, by E. V. Cowdry. It is a readable, personal account, based on a lifetime of experience, and as such is a good, general biography of the cells involved in unregulated growth.

The last section of the book is concerned with cell growth and development. J. P. Chang deals with the enzymatic behavior of hepatic cells in chemically induced cancers. W. R. Duryee discusses the nuclear physiology of amphibian adenocarcinoma and shows that an abnormal nucleolar activity is readily evident. M. Harris and F. H. Ruddle find no consistent patterns of chromosomal alterations which parallel drug-resistant strains of pig kidney cells. J. H. Taylor again reviews the duplication of chromosomes in the cell cycle as revealed by isotope studies and as compared with the light microscope and electron microscope findings, and reports on the difficulties of fitting all of the observations, both genetic and cytological, into a meaningful picture. R. Kinosita and S. Ohno discuss the problem of cellular differentiation as it takes place at the time of division, so that the two daughter cells are unlike the mother cell from which they arose. And T. J. King and R. G. McKinnell reveal newer data on the developmental potentialities of nuclei transplanted from renal cancer cells to enucleated eggs. M. J. Kopac then summarizes the symposium, rephrasing the questions and answers which the participants have brought out in their individual talks.

C. P. SWANSON

BEHAVIOR GENETICS.

By John L. Fuller and W. Robert Thompson. John Wiley & Sons, New York and London. $8.95. x + 396 pp.; ill. 1960.

John L. Fuller is a Senior Staff Scientist and Assistant Director at the Roscoe B. Jackson Memorial Laboratory at Bar Harbor, Maine. W. Robert Thompson is Professor of Psychology at Wesleyan University.

Fully one-third of the monograph is devoted to general principles of genetics, experimental methods in behavior genetics, and methods in human genetics, particularly human behavior genetics. This feature of the book will undoubtedly increase greatly its usefulness as a textbook and a reference book for those with little previous training in genetics.

The later chapters of the book treat in a systematic manner those characteristics relating to the nervous system. The titles of these chapters are as follows: Variation in sensory and perceptual processes; Response processes; Intellectual abilities; Personality and temperament; Mental disorders; and Heredity and individual differences in behavior.

Extensive references and good author and subject indices are provided. The book is primarily a review of work in the areas indicated by the table and chapter headings.

VICTOR A. MCKUSICK

THE LIFE AND DEATH OF CELLS.

By Joseph G. Hoffman. Dolphin Books, Doubleday & Company, Garden City. Ninety-five cents (paper). 354 pp.; ill. 1961.

I am pleased to see this excellent book appear in a paperback edition, and thus brought into the economic range of every student of biology. With the present flood of books coming out in the area of cellular biology, and with most of them so highly specialized and so technical in approach, it is well to have the generalist take a broad look at things, and to infuse readability, personality, and informality into a fast-moving, jargon-filled, but centrally important field of modern, experimental science. Hoffman does just this, and in fine fashion.

C. P. SWANSON

GENERAL AND SYSTEMATIC BOTANY

THE LICHEN FLORA OF THE UNITED STATES. *A Reissue.*

By Bruce Fink; completed for publication by Joyce Hedrick; new foreword by Alexander H. Smith. The University of Michigan Press, Ann Arbor. $12.50. xii + 426 pp. + 47 pl.; text ill. 1960.

The reviewer did not look forward to this assignment with pleasure, but what has to be said of Bruce Fink's *Lichen Flora of the United States* is not intended as criticism of the scientist, whose contributions to the science of lichenology are well known and respected. Fink's manual has long been the accepted text in American lichenology; its existence, indeed, has discouraged the publication of other competitive lichen floras because there are many who still astigmatically view the discipline as a specialized limbo of botany, too limited in workers to afford a companion work. The higher priced reissue could not be intended to attract buyers among students, and it is not likely that professionals will have need to reinvest in a facsimile volume. It is most regrettable that Fink's work has been reissued. This action was unjust to the memory of its author and an unintended but a strong suggestion to our more critical European colleagues that American lichenology has not advanced in the last 25 years. *The Lichen Flora of the United States* served its purpose in its time; in its present unrevised state, it should have been permitted to languish into classical respectability.

The matter is better understood when one recalls that the finished manual appeared 8 years after Fink's death. *The Lichen Flora of the United States* was an outgrowth of Fink's successful experience with *The Lichens of Minnesota* (1910); and in its present form, the manual offers the user a somewhat enlarged, but not always clearly focused view of the lichen flora of the rest of the states. Now that Hawaii and Alaska have been admitted to statehood, should they not be given consideration in a standard text? In the case of Hawaii, the problem is practically solved by Magnusson's extensive studies of the islands' lichen flora. Furthermore, our present adequate knowledge of the arctic lichen flora and the pressure of the widespread interests in Arctic vegetation make it imperative that serious consideration be given, not only to Alaska, but to all of the American Arctic.

The value of any taxonomic floristic manual lies in its usefulness and on that basis it must be said that Fink's manual is not altogether successful. There is a lack of clarity and decisiveness in descriptions at all diagnostic levels and an inconsistency and often confusion in the keys of even the larger and better-known species which frustrates the beginner. Obsolete names, many errors in species diagnosis, and the general nomenclatural inconsistencies block efforts to recognize genera or species. One has no choice but to turn to the older European literature where, thanks to the universality of many of these plants, one may resolve in simple and neat descriptions the problems of identification. The European sources are many and serve as examples of why lichenology has always attracted a larger following abroad. These include Lynge's *Study of the Lichen Flora of Norway*, Smith's *A Monograph of the British Lichens*, Harmand's *Lichens de France*, Andre's *Die Strauch- und Blattflechten Nordböhmens*, and not the least Magnusson's small but singularly precise handbook *Flora över Scandinaviens, Busk-och Bladlaver*.

Our present knowledge of the lichen flora of the United States is far from complete, and almost every European lichenologist who visits America finds new species and leaves us the wiser in their interpretation of the phytogeographical amplitude and richness of our flora. Within the last 20 years, as the Foreword to the reissue tells us, the number of specialists in this field has increased, but what it fails to add is that with this renascence of popularity, the proficiency of American lichenologists has grown to a very respectable degree. Inevitable changes in nomenclature and classification have been made by foreign and American lichen taxonomists and our appreciation of the phytogeographical and ecological characteristics of this class of plants has accumulated to a point where the present manual can no longer contain them. Consequently, one wonders how the decision to reissue Fink's manual could have been agreed upon—without thought to the appreciable increase in knowledge in this field; without feeling for the floristic magnitude of the lichen flora of the United States; without reference to the invigorating studies that have taken place since Fink's death; or without the least effort to update those parts which have been most recently revised. How, for example, can one possibly overlook the late A. W. Evan's contributions to our understanding of the manifold Cladoniae of North America?

With a reviewer's privilege, I should like to comment on the group I know best, the Umbilicariae, under which Fink groups 3 genera. With the exclusion of *Dermatiscum*, which has been questioned, the keys in Fink's manual list 22 species; these include 2 synonyms, 3 obsolete names, and 1 European species unknown in North America. The possibility of arriving at a correct determination of American material with the present keys is almost hopeless. In addition, we now count 26 species in this family. Similar confusion from inept keys and deficiencies

owing to the increase in the number of species recently described are also apparent in other families, viz., Pyrenulaceae, Lecideaceae, Lecanoraceae, Peltigeraceae, and Stictaceae. Motyka's monograph of *Usnea* describes over 70 species in the United States; Fink's manual lists about 6 species. Hale's work on the *Parmelia* has more than doubled the number of species reported in the United States by Fink.

The need for a modern manual in lichenology is a crying one. The task should attract the assistance of all our lichen specialists for collaboration in preparing a manual that should include all of North America and provide a work to match the many higher plant floras. It should be so printed that individual sections can appear in inexpensive paperback editions, so as to attract the widest audience and serve usefully the amateur, student, and professional in the Western Hemisphere.

GEORGE A. LLANO

PLANT PHYSIOLOGY

PHYSIOLOGY OF TREES.

By Paul J. Kramer and Theodore T. Kozlowski. McGraw-Hill Book Company, New York, Toronto, and London. $12.50. xiv + 642 pp.; ill. 1960.

"This volume represents the only up-to-date compilation of what is known about the physiology of tree growth." This statement on the front flap of the cover is perhaps the best description of the book that can be given in one sentence. The following chapters make up the 535 pages of richly and well illustrated text: Growth and structure; Photosynthesis; Carbohydrate metabolism; Nitrogen relations of trees; Fats, oils, terpenes, and related substances; Assimilation and respiration; Translocation and accumulation; Mineral nutrition and salt absorption; Water relations and transpiration; Absorption of water and ascent of sap; Internal water relations; Reproduction; Physiology of seeds and seed germination; Internal factors affecting growth; Environmental factors affecting growth. The text is followed by a very helpful list of common and scientific names mentioned in the text, a bibliography containing over 1,700 references, and author and subject indexes.

Büsgen & Münch's *The Structure and Life of Forest Trees* appeared more than 30 years ago, and there was consequently a definite need for a new textbook on tree physiology. Two types of books could possibly fill such a gap. On the one hand, there is the tightly knit textbook consisting of a synthesis that brings out the fundamental functional aspects of tree growth. Impact of presentation in such a book would necessarily demand a restriction of the number of citations to a relatively few selected examples. A literature review (or bibliography), on the other hand, would aim at completeness. This latter task has already been accomplished by one of the authors (T. T. Kozlowski: *Tree Physiology Bibliography*, University of Massachusetts, Amherst, Mass., 1956). In the present volume perhaps an unfortunate attempt has been made to combine the advantages of a textbook with the completeness of a bibliography. The discussion of 1,700 references in 535 text pages that include a great many tables and figures, as well as some basic information on plant physiology, has necessarily resulted in a more or less successful accumulation of 1,700 small pieces of information. For this reason a student might get the impression that studying tree physiology is identical with memorizing a great number of observations.

The main emphasis of the book is placed on environmental effects on the growth of trees. The reader interested in these aspects will find a wealth of information and accurate citations which make it possible for him to find his way quickly into the literature of any particular subject.

MARTIN H. ZIMMERMANN

LA CULTURE DES TISSUS VÉGÉTAUX. *Techniques et Realisations.*

By R. J. Gautheret. Masson & Cie, Paris. 10,500 fr. iv + 882 pp.; ill. 1959.

The field of plant tissue culture, like so many other fields of scientific research, having developed slowly during its first years, has seen an almost explosive expansion over the past decade. Gautheret, who has contributed through his own researches and through his students very largely to that development, has chosen at this juncture to examine in extenso the present status of the discipline and to provide students and investigators with an up-to-date compendium of methods and an acquaintance with current applications.

Probably no one knows the field better than he and, with certain limitations, he has done a masterly job. The book is an encyclopedia as well as a handbook. It is divided into 6 major parts: I. Techniques (7 chapters); II. Morphogenesis (2 chapters); III. Polarity and Induction (3 chapters); IV. Physiology (3 chapters); V. Cultivation of isolated cells (1 chapter); and VI. Pathology (3 chapters). All of these are examined in great detail, with a wealth of illustrative material. The chapters on Morphogenesis and on Polarity and Induction, covering as they do aspects to which the author has devoted particular attention in his own researches, are excellent and are particularly to be recommended. The sections on Techniques are very extensive and detailed but are less satisfactory, since many unimportant methods are given equal attention with classical ones.

The student may have difficulty in distinguishing them.

The book is a thoroughly French one, with all the virtuosity and at the same time the lack of balance which we have come to expect of such works. The framework of the subject is laid and the 50 years of its history reviewed in 7 profusely illustrated pages in which only 3 currently active workers with plant tissues are mentioned—the author, this reviewer, and one other. The uninitiated reader is thus left with little notion of how the field has arisen and with little basis for orientation with respect to what follows. And in what does follow the emphasis is placed so strongly on work done and methods used in the author's own laboratory that, although many other studies are mentioned, the reader can gain only an uncertain judgment of their relative importance. One result is a frequent failure to soundly evaluate work from other laboratories, sometimes to their detriment and sometimes quite the contrary. As an example, in the list of 147 strains of tissue listed (pp. 40–57) as isolated in culture and presumably available for study, there is at least one which was never successfully established (*Ipomea pandurata*). A more careful reading of the original paper would have shown this. These are merely symptomatic.

The book will long be an indispensable reference work for all investigators in the field. But the reader should be warned not to expect of it absolute completeness nor complete impartiality. The price of $24.00 will probably preclude any wide distribution to students, but every library should have a copy. It will be widely used.

PHILIP R. WHITE

ECONOMIC BOTANY

PLANT VIRUSES. *Methuen's Monographs on Biological Subjects. Third Edition.*

By Kenneth M. Smith. John Wiley & Sons, New York; Methuen & Co., London. $3.00. xii + 209 pp.; ill. 1960.

Most botanists, and particularly those associated with pathology, will be familiar with the first or second edition (*Q.R.B.*, 25: 351, 1950) of this book. Smith has now brought it up to date with much of the later literature, including the electron microscopy of viruses, incorporated into the text. Its usefulness, however, is still restricted to the plant pathologist, or to those who might need the information relative to the handling of viruses, for Smith has restricted himself to considerations of symptomatology, dissemination, vectors, latent infections and methods of inoculation, testing, serology, purification, and control. The recent genetic information derived from viral studies is not mentioned.

C. P. SWANSON

AN INTRODUCTION TO INDUSTRIAL MYCOLOGY. *Fifth Edition.*

By George Smith; foreword by Harold Raistrick. Edward Arnold, London; St Martin's Press, New York. $10.00. xvi + 399 pp.; ill. 1960.

Although following closely the subject and format of the fourth edition, (*Q.R.B.*, 30: 175. 1955), George Smith's new edition of *An Introduction to Industrial Mycology*, includes much valuable new literature on systematic mycology, particularly in reference to the fungi of industrial importance.

The industrial mycologist will be made aware of a number of changes in taxonomy since the fourth edition. Taxonomical names no longer tenable have been omitted or replaced with correct classifications; for example, *Sordonia destruens* is omitted because the original specimen was a mixture of *S. fimicola* and other ascomycete. Other changes in the fifth edition include descriptions of the genera *Phialophora* Medlar, *Scopulariopsis* Bainier, the species *Aspergillus echinulatus*, etc.

The fifth edition has a number of excellent and useful photomicrographs. In most instances, the new or replacement photomicrographs are superior to those in the fourth edition. They are well placed so that one can read the text description and examine the picture or drawing on the same page.

The section on laboratory equipment and technique is detailed and complete. By following the laboratory recommendations, it would be possible for a worker with only minimal training but familiar with biology to isolate, grow his organism in pure culture, and attempt partial classification of his particular fungus.

The laboratory worker who handles molds but does not consider himself a mycologist, as is true with so many of us in industry, will find this a valuable and necessary reference work.

ARTHUR R. ENGLISH

PLANT PATHOLOGY. *An Advanced Treatise. Volume II: The Pathogen. Volume III: The Diseased Population. Epidemics and Control.*

Edited by J. G. Horsfall and A. E. Dimond. Academic Press, New York and London. $22.00 (each). (Vol. II) xiv + 715 pp.; ill.; (Vol. III) xiv + 675 pp.; ill. 1960.

These volumes complete a three-volume compilation of various aspects of the science of plant pathology. The first volume has been reviewed (*Q.R.B.*, 35: 149. 1960). The second volume contains excellent chapters on multiplication of viruses, reproduction

of microorganisms, spore germination, mechanics and chemistry of penetration, toxic metabolites, and genetics of pathogenicity. The title of the second chapter, The Nature, Origin, and Evolution of Parasitism, is misleading, since its substance has to do with a classification of plant disease on the basis of effects rather than causes and has little or nothing to do with evolution. The last 4 chapters are concerned with various aspects of chemotherapy.

The third volume contains chapters on inoculum potential, dispersal of pathogenic agents, the nature and forecasting of epidemics, quarantine measures, and various methods of plant disease control. Most of these chapters lack conciseness. They leave the reader with the general impression of a grand marshalling of facts, as such, without serious attempt to put them into a useful arrangement and evaluate them as to their merit. Outstanding in this defect is the chapter on Cultural Practices in Disease Control. It has all the earmarks of the work of an armchair pathologist who has combed the literature for minutiae to fit into a prearranged pattern without any attempt to evaluate them. The last chapter, on The Problem of Breeding Resistant Varieties, is a good day-by-day account of cereal and flax breeding at the Minnesota Station, but the reader should know that it is just that and is far from a comprehensive treatment of the subject such as the title indicates.

J. C. WALKER

PLANT PATHOLOGY. *Laboratory Manual. Second Edition.*

By J. P. Fulton, D. A. Slack, N. D. Fulton, et al. Burgess Publishing Company, Minneapolis. $3.00 (paper). x + 95 pp. + 18 pl. 1960.

This is a manual for beginners in the study of plant diseases. It is designed to guide the student in his laboratory studies. For each disease the most essential facts as to symptoms, the nature of the causal organism or virus and its disease cycle, and methods of control, are presented in concise form. Various phases are illustrated by line drawings. The examples are drawn from diseases of various crop plants incited by bacteria, fungi, nematodes, and viruses. Non-parasitic diseases are not included. While some may criticize this manual for containing too much "spoon-feeding," the reviewer does not take this stand. The success of teaching, in the last analysis, will always reside with the instructor and not with the mechanism. If this manual is used properly to guide the student into a wrestling match with the basic underlying principles of the superficial facts that are presented, it can be a very useful tool.

J. C. WALKER

GENERAL AND SYSTEMATIC ZOOLOGY

MAMMALS OF WISCONSIN.

By Hartley H. T. Jackson. The University of Wisconsin Press, Madison. $12.00. xiv + 504 pp.; ill. 1961.

Hartley Jackson hardly needs to be introduced to any mammalogist, for he has been a prolific writer in mammalogy for many years. He is a native of Wisconsin, and this book is the result of many years of work there. The State of Wisconsin and the U. S. Biological Survey jointly sponsored much of the study, which proceeded intermittently for approximately 40 years.

In all, 19 families and 70 full species are now known to comprise the Wisconsin mammal fauna. For the reader interested in identification there is a key to the orders, and for orders containing more than one family there are keys to the families. Keys to genera and species as a rule are not provided. However, for each species there is given ample information for exact identification.

Much of the book is devoted to the natural history of the species. Here Jackson's breadth of experience permits treatment of a scope rarely equalled by any others. All known aspects of the life history of each species are covered, and many discussions are supplemented by illustrations. Diagrams of burrow systems, drawings of tracks, scats, feet, etc., provide much useful information. Diseases, parasites, and economic considerations are also discussed. The format of the book is most pleasing, especially the quality of the illustrations. The line cuts are beautifully clear, and the halftones so finely screened that they appear to be photographic reproductions.

The reviewer has detected only one gross error, which is obviously typographical; the inversion of the premolar formula for *Zapus* makes it seem that the mouse has a lower premolar rather than an upper.

A 46-page bibliography will be of value to future students of the Wisconsin fauna. Persons interested in mammalian habits, behavior, and life history will find the book a valuable reference and a milestone in natural history writing.

BRYAN P. GLASS

THE RECENT MAMMALS OF ARIZONA: THEIR TAXONOMY AND DISTRIBUTION.

By E. Lendell Cockrum. The University of Arizona Press, Tucson. viii + 276 pp.; ill. 1961.

In this book Cockrum has brought together all of

the published records of mammals from the state of Arizona, and added many of his own, to produce a complete state checklist. In addition to the usual items of a checklist, there are included an identification key, distribution maps for all species, and a complete list of specimens examined or recorded in the literature. Since the author has made an effort to examine personally all the larger collections from the state, the list is a virtual catalogue of the existing specimens of mammals from Arizona. In all, 292 subspecies of 137 species are recorded, a total not exceeded in any other state except adjoining California. To the list of known forms is added a list of species or subspecies expected for the state but whose presence has not been verified. There are 29 of these. The book, therefore, serves as an up-to-date checklist, a handy reference on distribution, and a stimulus to future study of the mammalian fauna of the Southwest.

BRYAN P. GLASS

A MANUAL OF COMMON BEETLES OF EASTERN NORTH AMERICA.

By Elizabeth S. Dillon and Lawrence S. Dillon. Row, Peterson and Company, Evanston, Ill., and Elmsford, New York. $9.25. viii + 884 pp. + 85 pl.; text ill. 1961.

A manual suitable for the identification of all the beetles of the Eastern United States has never existed. The closest approach has been Blatchley's *Coleoptera of Indiana* of 1910, which has been long out of print, lacked many species of the East not occurring in Indiana, and represented a rather antiquated treatment. The present manual offers a vast improvement, even if it does not represent yet the ideal solution, as it deals only with about 1,200 of the perhaps 10,000 species occurring in this region. The most common or most noticeable species have been selected, and there is a more than even chance that a beetle picked up by a casual collector will be found in this manual. Demanding completeness for this largest order of insects would be asking too much of any author at this time and would perhaps be more than the ordinary collector could take.

After some general remarks about collecting, ecology, structure, and illustrations of typical larvae, a key to the families is given followed by a treatment of the individual families, genera, and species with keys down to the species. The various diagnostic structures are well illustrated, so that the keys are easily understood. Figures of all the treated species, in general well executed, make it easy for the beginner to find and recognize a species better than any description in words can give a good idea of shape and ornamentation.

The book ends with a glossary and an extensive bibliography. The latter enables the more serious student to find the specialized monographs and papers dealing with special groups and which are necessary if one wants to deal with all the species in a particular region, or in a family or genus. It reminds the professional of the need of a modern revision of innumerable groups.

Obviously in a work of this kind it would be foolish to expect no mistakes or expect an infallible recipe for the easy identification of all beetles that might be found in this part of the country. One recognizes in many keys those of Blatchley which were taken in turn from Horn and Leconte and date back to the eighties.

There are a few omissions that are to be regretted. More biological and ecological notes would have been very welcome to those who are not merely interested in the beetles as museum specimens, as well as data on the approximate dates when the adult beetle can be found. Finally, some indication of the geographical distribution would also have been useful. One realizes that it would not always have been easy to provide complete data of this kind, but the public would have forgiven the authors inevitable mistakes if the attempt had been made to supply them. In the bibliography some omissions were noted. For instance, the papers of Dawson on *Serica* are missing, without which an identification of the species of that genus would be impossible; nor does one find the monograph of Leng on *Brachyacantha*.

The book is printed on good paper and sturdily bound. It certainly should be in the possession of everyone interested, be it seriously or only casually, in the beetles of this region.

G. H. DIEKE

THE BEETLES OF THE UNITED STATES. (*A Manual for Identification*). *Section 1.*

By Ross H. Arnett. The Catholic University of America Press, Washington. $3.50; $3.95 (loose-leaf binder). xii + 210 pp.; ill. 1960.

After many years without a beetle manual for the United States, here is a second one. It differs substantially from that of the Dillons' (see preceding review) in content, aim, and execution. In the first place, it is more sophisticated and will perhaps be of more value to the serious student than to the beginner or casual collector. It deals only with genera (including subgenera) and higher taxa and does not deal at all with individual species.

The author declares the book to be a revision of Bradley's *Manual of the Genera of Beetles of America, North of Mexico* which appeared in lithoprinted form in 1930. Actually, the only thing the new book has in common with the old one is that

both provide keys with which the beetle genera can be identified. In Arnett's book the keys are well illustrated with figures that should make them much easier to use.

There is first a key to all the beetle families of the whole world. Then the individual families are taken up with keys to subfamilies, tribes, genera, and subgenera. The part that has appeared contains the Cupedidae and the Adaphega. Notes on the taxonomic history, the biology and ecology, the geographic distribution, the number of species found in the United States, etc., for the family and each individual genus add considerably to the value of the book.

The bibliography is extensive. The general works are listed after the family key and there is a list after each family. References with each genus or tribe make this list easier to use, which is an advantage in the large families. (There are, for instance, 187 titles for the Carabidae).

Specialists have prepared some of the material or have checked it, a fact which will enhance its authenticity. Arnett has followed, with some deviations, the system of classification of Crowson which is reasonably conservative.

The bulk of the first part contains the family Carabidae, which takes up 127 pages. Here a comparison with Dillons' manual, where the corresponding material takes up only about 6 pages, shows the difference between the two works. Comparison with Bradley and other sources of older keys shows that the keys have been considerably reworked, and one hopes, improved. Only long use can show whether this is true.

There is one figure of a complete beetle for each family, which is not enough to give the uninitiated an idea of the often varying shapes. The reader needing this information will do well to use the figures in the Dillons' book for the East and in Hatch's *Manual for the West* for supplementary figures.

With all the care the author has used to give a reliable and authentic presentation of the North American beetle genera, it is a pity that he did not list the type species for each genus, even if that information necessarily had to be incomplete. There is a separate index for each family. It is to be hoped that there will be a general combined index when the whole work is finished.

The appearance of this book has made the study of American beetles infinitely easier. It is to be hoped that it will be followed by complete modern monographs of genera and families which will make the actual identification of species possible. One such monograph is that of the following review.

G. H. DIEKE

A REVISION OF THE GENUS *Diplotaxis* (COLEOPTERA, SCARABAEIDAE, MELOLONTHINAE). *Pt. 2. Am. Museum Natural Hist., Vol. 120, Art. 2.*

By Patricia Vaurie. American Museum of Natural History, New York. $5.50 (paper). iv + pp. 165–433; ill. 1960.

This is the second and final part of the revision of this genus which occurs in North and Central America. This part contains a key to all the species and a detailed description of 154 of the 220 known species. The remaining 66 were treated in Part I. Among these are 48 new species. The center of distribution of this genus is in Mexico. Ninety-seven species are known from the United States, 17 from east of the Mississippi.

On the whole, this is a difficult genus, as many species look alike. The male genitalia are not nearly as differentiated as in *Serica* and *Phyllophaga*, but without them an identification would often be virtually impossible. The monograph is a thorough professional piece of work.

G. H. DIEKE

BIONOMICS, SYSTEMATICS, AND PHYLOGENY OF *Lytta*, A GENUS OF BLISTER BEETLES (COLEOPTERA, MELOIDAE). *Illinois Biol. Monographs: No. 28.*

By Richard B. Selander. The University of Illinois Press, Urbana. $5.50. vi + 295 pp.; ill. 1960.

This is, in the first place, a monographic revision of the genus *Lytta* of North America in which the author includes what has been called the genus *Pomphopoea* LeConte as subgenus but from which he excludes certain Central and all South American species formerly placed in *Lytta*. He also discusses the taxonomic and phylogenetic status of the Old World species of *Lytta* without, however, giving a detailed description of them. Most of the American species occur in the West. Only the subgenus *Pomphopoea* is found east of the Mississippi.

The beetles of this genus, like most others of the family Meloidae, contain the irritant drug cantharidin which is obtained commercially chiefly from the European blister beetle, *Lytta vesicatoria*. The adult beetles feed on plants and are sometimes minor pests, but the larvae are interesting in that they are parasitic in the nests of wild bees with four different forms of larvae, the first very agile, adapted to find and attach itself to a bee and thus be transported to the nest where it changes into grublike form that is followed by two other forms before pupation.

The book contains many biological and ecological data and excellent distribution maps for each species. The author tries also to give the phylogenetic development of the species, and the nature of the

subject makes this part much more speculative than the rest.

The book is a very welcome and unusually complete contribution to the knowledge of American beetles.

G. H. DIEKE

A REVISION OF THE SPECIES OF *Schizonycha* DEJEAN (COL.: MELOLONTHIDAE) FROM SOUTHERN AFRICA. *Bull. Brit. Mus. (Nat. Hist.) Entomol., Vol. 9, No. 2.*

By R. D. Pope. British Museum (Natural History), London. 50s. (paper. ii + pp. 65–219 + 14 pl. 1960.

This monograph deals with about 120 species of this genus occurring in Southern Africa. The genus contains a total of more than 300 species. The paper contains keys to the species, detailed descriptions, many drawings of male genitalia, and other material which one expects to find in a monograph of this type.

G. H. DIEKE

A MONOGRAPH OF THE IMMATURE STAGES OF NEOTROPICAL TIMBER BEETLES (*Cerambycidae*).

By E. A. J. Duffy. British Museum (Natural History), London. £6 6s. viii + 327 pp. + 13 pl.; text ill. 1960.

This monograph gives descriptions with keys of larvae and pupae of cerambycid beetles of Tropical America. Biological notes are included and occasionally the adults are described and illustrated. Particular attention is paid to economic damage to valuable timber and fruit trees and to control measures. Much of the material in the book is new, the rest collected from various sources in the previous literature. The monograph is strongly oriented toward the economic aspects but gives also much material for systematic studies. For a little explored region like South America one cannot yet expect anything like completeness.

A similar monograph on immature Cerambycidae of Britain (*Q.R.B.*, 29: 268. 1954) and one of Africa (*Q.R.B.*, 33: 77. 1958) by the same author has appeared previously.

G. H. DIEKE

NEW CALEDONIAN LAND AND FRESH-WATER SNAILS. *An Annotated Check List. Fieldiana: Zool., Vol. 41, No. 3.*

By Alan Solem. Chicago Natural History Museum, Chicago. $2.50 (paper). ii + pp. 415–501; ill. 1961.

THE CULICINE MOSQUITOES OF THE INDOMALAYAN AREA. *Pt. V. Genus* Aedes *Meigen, subgenera* Mucidus *Theobald,* Ochlerotatus *Lynch,* Arribalzaga and Neomelaniconion *Newstead.*

By P. F. Mattingly. British Museum (Natural History), London. 15s. (paper). 62 pp., ill. 1961.

THE CICINDELIDAE OF CANADA.

By J. B. Wallis. University of Toronto Press, Toronto. $5.00. xii + 74 pp. + 4 pl.; text ill. 1961.

MOLLUSCS. *An Introduction to their Form and Functions.*

By J. E. Morton. Harper Torchbooks, Harper & Brothers, New York. $1.40 (paper). 232 pp.; ill. 1960. (A copy of the first (1958) edition.)

THE WORLD OF INSECTS.

By Paul Pesson; translated by R. B. Freeman. McGraw-Hill Book Company, New York and Toronto. $15.00. 204 pp. + 16 pl.; text ill. 1959.

The immediately striking thing about this book, its superb illustrations, remains its main forte after closer examination. There are over 200 photographs and 16 plates in this oversize book in full and clear color. The volume is a scattered sampling of the fantastically diverse and adaptive "insect world." Brief glimpses are presented of a bewildering number of the variations and specializations in structure and behavior which so abound among the members of the Class Insecta. The text, which ties these many facets together, is rather formal and scientific and lacks ease of reading. The reader is recompensed by the choice of intriguing, often extreme, examples and the opportunity to consult directly the excellent photographs, which serve to emphasize the general biological principles upon which the author bases his description.

PHILIP E. HARTMAN

ECONOMIC ZOOLOGY

THE INDIGENOUS LIVESTOCK OF EASTERN AND SOUTHERN AFRICA.

By I. L. Mason and J. P. Maule. Commonwealth Agricultural Bureaux, Farnham Royal, Bucks, England. 45s. xvi + 151 pp. + 179 pl. + 3 folded maps; text ill. 1960.

The staid title and contents of this work may lead it to pass unnoticed, except by specialists, in the flow of Africana that currently calls for attention; this would be a great pity, since it is undoubtedly one of the most important and valuable books on Africa that has been published in recent years. Many

of Africa's societies are wholly or in part dependent upon their livestock resources, yet little general account of these has so far been available. Even where search is made through scattered journal material, the accounts concerned are in several languages; much valuable material is in manuscript or in reports of limited circulation; and as much again is locked in the heads of men whose lengthy and close experience of African livestock has seldom been committed to paper at all.

Mason and Maule have attempted the enormous task of piecing together all available material on all domestic stock except fowl for the entire area south of Egypt and west of the Congo (though Ruanda Urundi and Angola are included). In this they have succeeded remarkably well. Their survey is accompanied by a six-language bibliography, which refers to English abstracts where they exist, and which includes numerous manuscript items and personal communications; several maps; and a remarkably thorough and clear range of livestock photographs. A good half of the volume deals with cattle; a matter which is justifiable in terms of their number and importance, but is also (one suspects) a reflection of the relative paucity of material on, say, the camel, which is of comparable importance in the northern part of the area covered. There are substantial sections on sheep and goats, and briefer surveys of the camel, horse, ass, and (briefest) the pig. Irrespective of their length, however, all the sections are clear, succinct, and of the greatest value.

The worth of the book lies not merely in its able survey of the literature, but in its authors' adoption of a trenchantly stated position from which the literature is viewed. *The Indigenous Livestock of Eastern and Southern Africa* thus has much more unity and clarity of treatment than is often found in survey compilations. Presumed historical origins of livestock groups are carefully avoided as a basis for their classification, in favour of surface and morphological characteristics which they hope are reasonably stable. This, of course, immediately introduces possible argument as to which morphological criteria are most valid: spinal bifidity and skull shape are rejected but hump size and location accepted for distinguishing between Sanga and Zebu cattle, for example, a procedure which may not be acceptable to everyone. As Mason and Maule note, blood types would be more satisfactory criteria from which to generalise, but they are as reluctant to do so from limited hemoglobin, or histological, data as they are from presumptive origin. Opting for the mass of gross data that veterinary surveys have yielded in the past, they present a classification based on animal types that utilises horn length, hump location and size, colour, and ear and tail conformation. Most commendably, they are meticulous in presenting previous classifications where they are at odds with their own, and even summarise these in tabular form.

It is pleasant to see tribal rather than political boundaries emphasized as the relevant territorial aspect of livestock groups. What may come as an innovation to readers of official reports is, however, nothing more than an implicit contention that domestic stock cannot profitably be surveyed without some reference to their domesticating agents. Tribal groups dependent on herding commonly select for specific patterns, colourings, and bodily conformations—especially in male breeding stock—for both economic and aesthetic reasons. While their selection methods may not be as rigorous as those of western breeders, they are as conscious; and it is difficult to believe that they do not have a pronounced effect on livestock types over a prolonged period. It could also well be borne in mind that most pastoral groups are militant and raid stock from each other: the absence of peaceful inter-tribal contact need not therefore imply (as stated) separate breeding populations of stock—it can as well indicate stock-mixing on a considerable scale.

In any work of this breadth, and as pioneer, it is to be expected that there may be minor defects. These reflect not the limitations of the compilers so much as the nature of the material with which they must deal. Indeed, it is surprising that there are not more noticeable shortcomings considering the magnitude of their task. It may serve as an example to take the area best known to me, however. 'Karimajong cattle' include 3 major domesticating groups—the Karimojong, Jie, and Dodoso tribes—as well as minor hill tribes only partly dependent on stock. Not all of these appear to select for the same cattle features. The Tepes on Mt. Napak, for instance, own cattle with spreading horns of the Ankole type, which Karimojong do not care for. The desired colour combination in Karimojong bulls is not among the types listed—being black forebodied with a grey/white trunk. Prize breeding bulls, as well as favourite oxen, can weigh in the region of 700 kg, which is twice the maximum estimate referred to. Brindled, roan, black, and reddish hides are found as well as the colours given, and the range of hide patterns is very great, as the native vocabulary attests.

There are other more general defects, though still of a minor kind. Ingessana should surely be Ingassana; the western limits of Somali and the position of Masai on the map on p. 128 could stand correction; it is misleading simply to say that "the Nilotic peoples expect no work from their cattle" when many of them subsist largely from their animals; nor is it yet proved, the figures for "native" herds being absent, that cattle of a local breed will necessarily yield under "native" conditions

than on government farms. Yet none of these minor points can detract from the fact that Mason and Maule have produced a major work, and produced it with great succinctness and clarity.

It is to be hoped that *Indigenous Livestock of Eastern and Southern Africa* will be revised as fresh information becomes available, for it has the marks of a book that will be with us for a long time to come. It should appeal to an extremely wide audience—veterinary specialists, conservationists, economic planners, sociologists interested in pastoral groups, and any government agency concerned with economic assistance to the countries of Africa.

NEVILLE DYSON-HUDSON

ANIMAL PHYSIOLOGY

ANNUAL REVIEW OF PHYSIOLOGY. *Volume 23.*

Victor E. Hall, editor; assoc. eds., Frederick A. Fuhrman and Arthur C. Giese. Annual Reviews, Palo Alto. $7.00. viii + 674 pp. + 1 pl. 1961.

Contents: Pharmacology in a changing world (C. F. Schmidt); Energy metabolism (M. Kleiber and T. A. Rogers); Transport through biological membranes (I. S. Edelman); Comparative physiology, photoperiodicity (D. S. Farner); Physiological aspects of aging in man (N. W. Shock); Respiration (S. M. Tenney); Digestive system (H. D. Janowitz); Liver (J. L. Bollman); Skin (W. C. Lobitz and F. Daniels); Adenohypophysis and adrenal cortex (E. B. Flink); Reproduction (J. T. Valardo); Peripheral circulation (D. F. Bohr); Heart (B. F. Hoffman and F. Kavaler); Excitation and conduction (K. Frank and M. G. F. Fuortes); Somatic functions of the nervous system (P. Buser and A. Rougeul); Visceral functions of the nervous system (G. Ström); Brain functions and learning (E. R. John); Hearing (M. Lawrence); Comparative physiology; transmitter substances (E. Florey); Major problems in muscle physiology (W. F. H. M. Mommaerts, A. J. Brady, and B. C. Abbott); and Kidney, water and electrolyte metabolism (H. Wirz).

MAMMALIAN HIBERNATION. *Proceedings of the First International Symposium on Natural Mammalian Hibernation, May 13–15, 1959. Supported by the Office of Naval Research and sponsored by the American Institute of Biological Sciences. Bull. Museum. Comp. Zool., Vol. 124.*

Edited by Charles P. Lyman and Albert R. Dawe. Museum of Comparative Zoology at Harvard College, Cambridge. $3.00 (paper). 549 pp.; ill. 1960.

This volume contains 26 papers, almost all of which deal with physiological changes in the hibernating animal. These include various endocrine activities, histological changes, brown fat, reproduction, cardiac function, vascular changes, peripheral nerve function, tissue respiration and metabolism, the biochemical changes. Oddly deficient are the topics of induction and termination of hibernation. As noted in the preface and as is evident from the text, only the beginnings of a physiology of hibernation have been made. A rather long discussion section ends the volume and points up many of the problems for the future.

DAVID R. EVANS

MARSHALL'S PHYSIOLOGY OF REPRODUCTION. *Volume I: Pt. 2.*

Edited by A. S. Parkes. Longmans, Green & Co., New York. $48.00. xx + 877 pp.; ill. 1961.

This is an important contribution by our British colleagues, worthy successors to the great F. H. A. Marshall and his teacher, Walter Heape. Three quarters of a century have thus been spanned by the three editions (1911, 1922, and 1960) of the *Marshall.*

The first chapter, numbered Chapter 7 (six chapters having appeared in Part One) might be characterized as "all about sperms." Not only have many of the details of structure of this fantastically complex cell been unraveled by both the light and the electron microscopes, but by means of staining techniques the biochemical nature of the organelles of the sperm have been identified, not only in the fully formed sperm, but in the course of its differentiation from the spermatogonium. Abnormalities are described and the results of deleterious external influences discussed. The dynamics of spermatogenesis are treated masterfully, including the spermatogenic cycle in the rat, with time relations for the completion of each of the 14 identifiable stages, a total of 40 days. No such exact details are yet known for man. The migration of sperm from testes to the vas deferens and the "maturation" of sperm within the male genital tract are briefly but adequately discussed.

In Chapter 8 the late A. Walton presents the basic facts of sex drive and describes natural insemination by copulation in various species of domestic animals. The chapter reveals the great variety of conditions and locus and manner of deposit of semen in the genital tract of the female, with resultant differences in the manner and rate of ascent of the sperms.

Chapter 9 is devoted to artificial insemination, including not only techniques adaptable to a variety of animal species (including honey-bee queens) but also data on the preservation of spermatozoa and their transport and survival in the female tract. As millions of cows are now being inseminated an-

nually with bull semen stored in the frozen state, "semen banks" from individual high-bred bulls are now a reality. Little success has thus far rewarded efforts in this direction with human semen. Contrariwise, some attention is paid to substances that inhibit the fertilizing capacity of sperm. Some of these chemicals and physical factors constitute contraceptives. A promising endeavor in this direction lies in the immunological reaction of sperms (e.g., agglutination) to parenteral injection of sperms.

Metabolism and motility of sperms are logically considered together in Chapter 9A. The probable metabolic pathways are clearly presented and factors, such as pH, temperature, dilution, hormones as they affect both metabolism and motility, are briefly discussed. This chapter also covers the significance of motility to fertility and to sperm migration.

Chapter 10 contains a comprehensive review of fertilization. The striking phase-contrast microphotographs lend charm and lucidity to the processes involved: reduction of chromosome number of the egg (the steps in polar body formation), mode of penetration of the zona and vitelline membrane (acrosome first), the metamorphosis of the chromatin of the sperm head into the male pronucleus, matching that of the female chromatin. These details are inimitably illustrated by microphotographs. New data are added on the probable function of the pronuclei. Examples are given of parthenogenic cleavage. The history of fertilization in vitro was written before Chang gave the final proof that this is possible with mammalian material.

There follows a most useful chapter on the anatomical structures associated with reproduction in the various sub-mammalian classes of the Vertebrata from the fishes to Amphibia and Reptilia. One is struck with the great variety of structures that serve the perpetuation of species.

This summary might well serve investigators as a guide for the selection of the species most likely to give the desired answers in special endocrine studies.

In Chapter 12 Parkes and A. J. Marshall furnish a review of the spectacular anatomical, behavioral, and developmental effects of hormones in birds. The marked sexual dimorphism of birds heads the class favorable for investigation into the endocrine control of sex characters, while the accessibility of the avian embryo in the egg makes it the ideal test-object for analyzing the endocrine control of the development of the primary and secondary sex characters. This situation also renders the bird adaptable to the production of hermaphrodites. The response of the bird comb or the bill to androgens is shown to be the basis for the assay of androgenic hormones. The behavioral (initiation of brooding) and crop-gland stimulating action of prolactin completes the chapter. The role of the endocrines in conditioning bird migration is more fully treated in the next chapter.

Details and neuro-endocrine relation of the diurnal and seasonal periodicity of response in animals to environmental influences are marshalled in Chapter 13. The built-in time clock that operates in a monotonous environment comes in for its share of attention. The modern concept of nerve paths to the pituitary gland via the hypothalamus is briefly touched upon. The seasonal factors in sexual periodicity are shown to apply to all classes of vertebrates. Estrous activity as well as seasonal breeding and even the urge to migrate (Zugunruhe) may be overridden by artificial illumination. The most effective wave-lengths of light have been identified. A short section is devoted to the meaning of sexual display and courtship in animals.

The ample bibliographies attached to each chapter (totaling some 5,000 entries) and the comprehensiveness of the items covered make this volume useful as a reference work; but many sections are "readable" for more than the recital of facts. The nearly 250 illustrations, mostly superb half-tones, contribute largely to the price of the book. By themselves they should be worth 20¢ apiece, the text being thrown in for good measure!

Errors in this volume are likely to be minor ones and no attempt was made to ferret them out.

The indexes are well done. As in other works so in this, it is discouraging to see over 30 page-references to a single author. In this book Witschi has 57, A. J. Marshall 70, A. J. Parkes, 79! A hasty trial with a score of items gives one the feeling that the subject index is quite satisfactory.

All of us will consult this work for a long time to come.

CARL G. HARTMAN

ANIMAL SOUNDS AND COMMUNICATION. *With 12-Inch Long-Playing Record. Am. Inst. Biol. Sci., Publ. No. 7.*

Edited by W. E. Lanyon and W. N. Tavolga. American Institute of Biological Sciences, Washington. $9.50; $8.50 (AIBS members). xiv + 443 pp.; ill. 1960.

Increasing interest in the sounds made by animals has undoubtedly come about as a result of the development of new instruments for recording and analyzing sound. In any event, the past few years have seen a number of symposia devoted to this field of study. The present volume is the proceedings of one such symposium. It is accompanied by a standard 12-inch LP record prepared from tape recordings that accompanied the papers delivered at the meeting. The book contains the following papers: Introduction (J. T. Emlen); Considerations and techniques in recording sound for bioacoustics studies (P. P

Kellogg); The analysis of animal sounds (D. J. Borror); Sound communication in Orthoptera and Cicadidae (R. D. Alexander); Sound production and underwater communication in fishes (W. N. Tavolga); The influence of sound on the behavior of amphibians and reptiles (C. M. Bogert); The ontogeny of vocalizations in birds (W. E. Lanyon); Bird songs and mate selection (P. Marler); An ecological and functional classification of animal sounds (N. E. Collias); and Logical considerations in the study of animal communications (C. F. Hockett).

As in all volumes of this sort, the quality is uneven; furthermore, the allotment of space does not seem to be tailored to the importance of the subject considered within the framework of the whole symposium. The analysis of animal sounds is treated in 10 pages; the paper on amphibian and reptilian sounds comprises 183 pages, about 40 per cent of the book. For anyone interested in animal sounds, reading this book constitutes a good entree into the subject. The accompanying record is clearly for scientific purposes.

VINCENT G. DETHIER

HYPOTHERMIA AND THE EFFECTS OF COLD. *Brit. Med. J., Vol. 17, No. 1.*

Introduction by O. G. Edholm. The British Council, London. $3.25 (paper). 78 pp. + 2 pl.; text ill. 1961.

ANIMAL NUTRITION

REACTIONS IN THE RUMEN.

By the late A. J. G. Barnett and R. L. Reid. Edward Arnold (Publishers), London; [St. Martin's Press, New York]. $9.00. viii + 252 pp.; ill. 1961.

No longer is the contented cow an animal which peacefully chews its cud, leisurely reflecting upon the pleasantries of life. On the old-time hay ration, she spent about 8 hours per day in operating the process of rumination. On a modern concentrate ration, she spends much less time in her favorite pastime. Thus, even the cow has succumbed to the pressures of modern living. She also has less privacy today than in the past. Her personal life has been investigated in every detail. Vast inroads have been made in the physiological aspects of this intricate system of feed, microorganism, and animal. This book tells the "inside story."

As the title to this volume indicates, emphasis has been placed on the reactions which occur in the rumen, and the mediators of these reactions—the microorganisms. There are sections on experimental methods used in ruminology; the microfloral content of the rumen; synthesis of fatty acids in the rumen; the utilization of carbohydrates, nitrogenous compounds, and various feeding stuffs in the rumen; and minerals, vitamins, and antibiotics as factors involved in rumen function. These factors are tied in with the physiology of the animal. Special attention is given to the structure and development of the rumen, and transport and utilization of fatty acids. The book is organized so that it might serve as a reference as well as a text. Extensive lists of citations, covering the literature into 1959, are given after each chapter. The book is quite similar in format to many of the current review series, including the presence of a complete author index and a rather adequate subject index.

Now the microbiologist, animal husbandman, and animal physiologist have the opportunity to catch up on what each other has done: in fact, anyone wishing to gain more insight into the animal sciences will find this book of interest. Regardless of how long the contented cow spends in chewing her cud daily, or what the cow is thinking about during this process of rumination, she is becoming more and more inept at keeping her secrets from us.

PAUL A. HARTMAN

ADVANCES IN FOOD RESEARCH. *Volume 10.*

Edited by C. O. Chichester, E. M. Mrak, and G. F. Stewart. Academic Press, New York and London. $13.00. xiv + 488 pp.; ill. 1961.

This series is a veritable smorgasbord of reading material. Volume 10 contains the following pleasurable offerings: red meats, other proteins, soy sauce, sauerkraut, potato chips, tropical and subtropical fruits, and paralytic shellfish poison. This menu is representative of the diverse interests which converge in the area of food research today.

That food science has developed during the past decade into a unifying, scientific discipline is well illustrated by the entree, a general review by M. A. Joslyn entitled, Research in Food Science and Food Technology: A Status Report. Food science as a research field is discussed, developments of the past 12 years which have resulted in maturation of food science as a discipline are described, and 12 major advances which indicate trends in the foods field are given. The second review follows more specific lines: a generous serving of Protein Chemistry and Food Research is offered by R. E. Feeney and R. M. Hill. Egg and milk proteins are selected for detailed discussion; however, meat and fish proteins are not neglected in this fine review. The next course follows the same lines, but is even more specific in nature. R. Hamm reviews The Biochemistry of Meat Hydration. This very thorough and timely review is of interest to many because the subject of meat hydration has both academic and economic implications. To enrich the flavor of the book is a review, by T. Yokot-

suka, on the Aroma and Flavor of Japanese Soy Sauce. Here emphasis is placed on the constituents of soy sauce which contribute to flavor, aroma, and stability, and how these constituents are affected by raw product and by process. C. S. Pederson, world's record holder for the manufacture of sauerkraut in the laboratory, treats the topic of Sauerkraut in a manner which results in a treat for the reader. The potato chip becomes more than an entremets under the careful scrutiny of the late H. D. Brown. This review, Potato Chip Processing and Technology, is a fine example of the point made by Joslyn: that food science is a hybrid of scientific disciplines. Culture, storage, anatomy, histology, and chemistry of the tuber are discussed; effects of processing conditions and additives on the tuber and chip are covered; sanitation, quality control, and waste disposal are examined; packaging and shipping are described; and nutritional qualities of the chip are enumerated. J. B. Biale allows the reader a taste of The Postharvest Biochemistry of Tropical and Subtropical Fruits. The effects of the composition of fruits on respiration and vice versa are given. E. F. McFarren and 5 co-authors team together to serve a dessert which consists of all phases of the Public Health Significance of Paralytic Shellfish Poison.

Smorgasbords are always interesting. This one is especially pleasing because the authors have all given comprehensive treatment to their areas, and have recorded their viewpoints on the pathways which are open to further scrutiny in food research. These factors combine to assure the reader that he will not suffer from mental malnutrition.

PAUL A. HARTMAN

BIOPHYSICS AND GENERAL PHYSIOLOGY

MATHEMATICAL BIOPHYSICS. *Physico-Mathematical Foundations of Biology. Third Edition. Vols. 1 and 2.*

By N. Rashevsky. Dover Publications, New York. $2.50 (per volume). (Vol. 1) xxvi + 488 pp.; ill.; (Vol. 2) xiv + 462 pp.; ill. 1960. (Reprint of 1960 edition (University of Chicago Press.).)

RADIATION PROTECTION AND RECOVERY. *International Series of Monographs on Pure and Applied Biology. Division: Modern Trends in Physiological Sciences. Volume 7.*

Edited by Alexander Hollaender. Pergamon Press, Oxford, London, New York, and Paris. $12.50. vi + 392 pp.; ill. 1960.

In a very real sense this book is a genuine reflection of the activities, interest, and direction of the Biology Division of the Oak Ridge National Laboratory. With the exception of Peter Alexander, who in the first chapter treats of macromolecular systems and their protection from the damage induced by ionizing radiations, all of the remaining authors are, or at some time have been, members of this group. The book is also a reflection of the leadership and stimulation of the division's director, who has acted as the editor, and who was among the first of the radiation biologists to recognize that an understanding of the protection against, and a recovery from, radiation effects is of both practical and theoretical importance. The practical considerations are obvious and must be pursued in an atomic age; the theoretical implications are of even greater importance, for our understanding of the fundamental action of radiations on biological material determines, in large measure, the limits of radiological science as an instrument of human welfare and the uses of radiation as a probe for the investigation of a multitude of other problems.

A wide gamut of problems is considered by the various authors: protection of macromolecules, genes, chromosomes, cells, and whole organisms from bacteria and fungi to mammals; experimental treatment of acute whole-body radiation injury; modification of delayed somatic effects; radiation and antibody formation; and photoreactivation. There is considerable variation in the skillfulness with which each subject is treated, but each on the whole is readable, well documented, and a good source of information. It is quite evident that while protection and recovery are possible in a number of ways, and that empirical procedures are useful, there is no good agreement as to the mechanisms involved. Much fundamental information must still be obtained if a complete understanding is to be had of both the action of ionizing radiations and the means whereby its effects may be offset.

If there is a criticism to be voiced of the volume, it is that there is no concluding statement that sums up the entire situation and that might have pointed out directions for future research. A concluding statement, for example, on the problem of radiosensitivity would have been fitting, even though it is realized that such a statement could have no finality about it.

C. P. SWANSON

THE STRUCTURE AND FUNCTION OF MUSCLE. *Volume II. Biochemistry and Physiology.*

Edited By G. H. Bourne. Academic Press, New York and London. $16.50. xiv + 593 pp.; ill. 1960.

The second in this series of 3 volumes contains articles by Albert Szent-Györgyi, D. M. Needham, E. C. Slater, June A. Russell, and Alfred E. Wilhelm on muscle proteins, biochemistry, and endocrinology. D. Nachmansohn reviews the role of acetylcholine at the neuromuscular junction. Muscle biophysics is treated by Robert W. Ramsey, and R. J. Podolsky presents a discussion of the thermodynamics of mus-

cle. The comparative physiology of smooth muscle is covered by C. Ladd Prosser, and Roger Bannister and E. H. Christensen review the physiology of muscular exercise. The central nervous system control of muscular contraction is detailed by Marion Hines and Mommaerts; Abbot and Whalen discuss various aspects of cardiac physiology. For the most part, the chapters on biochemistry are well done, and they cover their respective fields up through 1958. The chapters on biophysics and physiology are complete as far as they go, which is through 1957. The book presents a comprehensive coverage of the basic facts and concepts of muscle physiology and biochemistry as they were developed during the thirties and forties and elaborated in the early fifties. Although there is an indication in the chapters on biochemistry that some of our basic facts and concepts may be in for a revision, there is little hint that this is also the case for muscle physiology, as is clearly indicated by recent studies. This volume may be appropriately called a complete history of the ATP–actomyosin–active-state era of muscle physiology. It is perhaps fitting that it should appear at the dawn of a new era which sees the active-state theory in need of major revisions, the role of ATP uncertain, and the exact size and structure of myosin the subject of controversy. The next few years will no doubt see this volume badly in need of revision.

FRANCIS D. CARLSON

THE STRUCTURE AND FUNCTION OF MUSCLE. *Volume III. Pharmacology and Disease.*

Edited by G. H. Bourne. Academic Press, New York and London. $15.00. xiv + 489 pp. + 20 pl.; text ill. 1960.

The student of muscular contraction will find this, the third volume of this series, an informative summary of the pharmacology and disease of muscle. S. Thesleff, N. C. Moran, and Marion dev. Cotten treat the pharmacology of smooth, striated, and cardiac muscle. There follow chapters on virus infections, parasitic infections, nutritional deficiencies, aging and post mortem changes of muscle, myopathy, and clinical and genetic aspects of muscular disease. The book concludes with some remarks by Albert Szent-Györgyi.

FRANCIS D. CARLSON

THE HARVEY LECTURES. *Delivered Under the Auspices of The Harvey Society of New York. 1959–1960. Series 55. Under the Patronage of the New York Academy of Medicine.*

By T. T. Puck and 7 other contributors. Academic Press, New York and London. $8.00. xvi + 257 pp.; ill. 1961.

Contents: Quantitation (sic) of growth of mammalian cells (T. T. Puck); Biological foundations of wound repair (P. Weiss); Neurotransmission in the adrenergic nervous system (U. S. von Euler); Iron metabolism and nutrition (C. V. Moore); Inside nucleic acids (P. Doty); Renal mechanisms for potassium excretion (R. W. Berliner); Role of N_2 gas in various biological processes with particular reference to the lung (H. Rahn); and The role of fetal hormones in prenatal development (A. Jost).

THE BIOLOGY OF AGING. *A Symposium held at Gatlinburg, Tenn., May 1–3, 1957, under the sponsorship of the AIBS and with support of the National Science Foundation. Publ. No. 6.*

Edited by Bernard L. Strehler with James D. Ebert, H. Bentley Glass, and Nathan W. Shock. American Institute of Biological Sciences, Washington. $7.75 ($6.75 AIBS Members). viii + 364 pp.; ill. 1960.

This volume is the report of a very large symposium on aging that was held about 3½ years before publication. Even though so dated, it contains many interesting papers and discussions. Occasional footnotes cite more recent results and references.

The first 100 pages are devoted to free-ranging discussions by the participants of some eleven, largely theoretical aspects of the problem. The comments have been thoroughly organized and edited, much to their benefit. While the ideas are preserved, the discussions have been pruned and rearranged around consistent themes. These sections, since they deal with some of the most vexing questions, contain many sincere differences of opinion; the exchanges make lively reading.

Following are theoretical and experimental papers individually presented by the participants. Somewhat disconcerting is the fact that the earlier discussion makes frequent reference to these papers, so that one who intends to read through the volume would be better advised to begin here and read the discussion sections later. The papers (about 50) range in subject over all aspects of aging.

A short appendix proposes several programs for the promotion of research in the area. Especially significant is the suggestion that a center be established from which investigators could obtain older or aged animals of several species, each of known age and strain. A suitable subject index concludes the volume.

Altogether, the book is an excellent report of the status of theory and experiment at the time of the symposium, and its equivalent has not appeared since.

DAVID R. EVANS

BIOLOGICAL CLOCKS. *Volume XXV. Cold Spring Harbor Symposia on Quantitative Biology.*

Foreword by Arthur Chovnick. The Biological

Laboratory, Cold Spring Harbor. $8.00. xiv + 524 pp.; ill. 1960.

This 1960 symposium contained more than 50 papers on biological clocks and related phenomena. They are grouped under the following headings: General Properties of Circadian Rhythms (C.Rs.); Metabolic Aspects of C.Rs.; Models for C.Rs.; C.Rs. in Photo- and Thermo-periodism; C.Rs. in Animal Physiology; Ecological Aspects of C.Rs.; Chronometry in Celestial Navigation; and Longer Periodicities. Both plant and animal systems are well represented. There is analysis of clocks from the subcellular, to the neural and endocrine, and to the organismal level. There are several theoretical treatments of biological clocks and possible model systems. Unfortunately, the schools of F. A. Brown and C. S. Pittendrigh never quite come to grips with their differences, though both presented papers and contributed to the printed discussion. Very well represented are the workers in animal navigation, and here the material ranges far afield from clocks as such. Several argumentative presentations evaluate the literature on diurnal and nocturnal bird navigation, as well as sun orientation by bees, and homing in fish.

The volume is of the usual high quality of the series. Having been published within 6 months of the symposium, the material is timely, an accomplishment publishers of other symposia rarely match.

DAVID R. EVANS

BIOCHEMISTRY

METABOLIC PATHWAYS (*Second Edition of Chemical Pathways of Metabolism*). *Volume I.*

Edited by David M. Greenberg. Academic Press, New York and London. $18.00. xvi + 572 pp.; ill. 1960.

Metabolic Pathways is the second edition of *Chemical Pathways of Metabolism* (*Q.R.B.*, 30: 82. 1955) both edited by D. M. Greenberg. The purpose of the work is to provide a definitive "... survey (of) the existing knowledge of the chemical steps of major importance in living organisms." The series provides a comprehensive reference source for workers and teachers in biochemistry and related fields.

The aims of the work are essentially fulfilled in all of the articles of Volume I with one exception: the chapter on Carotenoids and Vitamin A by G. Mackinney. Half of this chapter consists of an uncritical duplication of the functions of carotenoids in such areas as photosynthesis, phototropism, and vision. This section is both poorly presented and irrelevant to the aims of the volume. The other half, on the metabolism of the carotenoids, is not written with sufficient clarity to be informative to any but experts in the field. A major defect is the use of names of numerous complex compounds without presentation of their structural formulae. Most of the discussion seems to be at the level of a sophisticated, critical appraisal of the conclusions arrived at in papers, the actual experimental work of which the author never describes.

The chapter on Free Energy and Entropy in Metabolism, by A. B. Pardee and L. L. Ingraham, is a remarkably lucid exposition of "... the concept of free energy ... (introduced) ... in a simple, descriptive way." This is not true of the section of their chapter dealing with entropy, which uses too many undefined words and concepts to be useful for a reader with only limited background. Similarly, an otherwise very fine chapter on Glycolysis, by B. Axelrod, fails to give sufficient background on the mechanism of action of triose phosphate dehydrogenase and of some other enzymes, so that extra reading is required to make that section comprehensible.

The Mitochondrial System of Enzymes, by D. E. Green and S. Fleisher, contains an organized description of the large body of impressive papers coming from the authors' laboratory, dealing both with the enzymes and the nature of their binding into the lipid-rich mitochondria. While the article is highly satisfactory in this and almost all other areas, it is deficient in its reporting of the vast body of literature on oxidative phosphorylation. The volume would have been more compete if it had included a separate article on the mechanism of oxidative phosphorylation, as well as this one on the enzymes of mitochondria.

There are no significant reservations about the caliber of the other chapters. They are all either very adequate or outstanding, and make this volume a required one for libraries, for teaching biochemists, and for any others who need a definitive source of information in intermediary metabolism. The other chapters include the following: The Tricarboxylic Acid Cycle (H. A. Krebs and J. M. Lowenstein); Other Pathways of Carbohydrate Metabolism (Bernard Axelrod); Biosynthesis of Complex Polysaccharides (W. Z. Hassid); Fatty Acid Oxidation and Synthesis (D. E. Green and D. M. Gibson); Ascorbic Acid (J. J. Burns); Metabolism of Phosphatides (R. J. Rossiter); Metabolism of Sterols (T. T. Tchen); and Metabolism of Steroid Hormones (L. T. Samuels).

A. T. JAGENDORF

THE BIOCHEMISTRY OF INSECTS.

By Darcy Gilmour. Academic Press, New York and London. $8.00. xii + 343 pp.; ill. 1961.

Comparative biochemistry is a recent approach to the study of biology seeking differences and similarities in those reaction systems upon which biological form and structure ultimately depend. In this

sense, a book on insect biochemistry is a limited part of comparative biochemistry. *Biochemistry of Insects* is written from a naturalist's viewpoint, emphasizing the chemistry of insects rather than stressing the mechanisms of biochemical reactions in insects.

The book is organized into 3 sections. The first of these, Energy Metabolism, groups together processes concerned primarily with the winning and expenditure of energy. Included in this section are discussions of nutrition and digestion, anaerobic and aerobic energy production, energy conservation and conversions, and end-products of catabolism. The second section, called Intermediate Metabolism, deals with the interconversions of compounds involved in processes other than those directly associated with the release and expenditure of energy. Chapters on the metabolism of carbohydrates, lipids, and nitrogen compounds are included in this division. Section 3, which consists of only 5 pages, deals with hormonal regulations of metabolism mostly in connection with metamorphosis.

This book is the first text on the biochemistry of insects and, as such, was needed for bringing together and summarizing the existing information. This, the book does moderately well. The discussions of the synthesis of phenoxazine pigments and quinone tanning of proteins, as well as sections on muscle metabolism, should be of special interest to the comparative biochemist. The entire book will be of value to entomologists and to those engaged in the related field of insecticide toxicology.

BERTRAM SACKTOR

NITROGEN METABOLISM IN PLANTS. *Row, Peterson Biol. Monogr.*

By George C. Webster. Row, Peterson and Company, Evanston and White Plains. $3.50 (paper). viii + 152 pp.; ill. 1959.

This monograph is potentially of value in filling a part of the real gap in texts on the biochemistry of plants. The chapters on nitrogen nutrition, biosynthesis of amides and peptides, and nitrogen metabolism in the intact plant fulfill this goal to a very considerable extent.

The section on amino acid metabolism is not so satisfactory, due mostly to the vast extent of this field. The pathways for synthesis and breakdown of all the amino acids are condensed to 35 small pages, so obviously the chapter is nothing but a breathless survey. In addition, most of the pathways discussed are found in animals or microorganisms, and their existence in plants is only inferred by analogy. Nevertheless, this chapter could be valuable to a student seeking orientation in the main outlines of this difficult field.

The chapter on protein and nucleic acid metabolism, the longest in the book, could be the most useful. It contains a critical, careful presentation of much of the work on protein biosynthesis. With the exception of the very fine contributions by the author himself, most of this work again has been done on bacteria or on mammalian tissues (the term "plant" is stretched here to include bacteria). Unfortunately the references extend only through 1957, and of course a great deal of important work done since then has cast an entirely different light on much of the preliminary material. Especially unfortunate is the author's strong emphasis on the concept that protein synthesis requires simultaneous synthesis of nucleic acids. This concept has only indirect evidence to support it, and certainly has not been borne out in work on the intimate mechanism of protein or nucleic acid biosynthesis accomplished since 1957.

As long as so much attention has been paid to protein biosynthesis, it would have been pertinent to include at least a brief mention of the existence of secondary and tertiary structure in proteins, and the problems of their organization. Also omitted completely is any mention of the synthesis of viruses, certainly a striking part of protein biosynthesis found in the plant kingdom.

One can hope for an early revision to correct these weaknesses due primarily to rapid advances in the field. An appropriate revised version would be extremely valuable as text material for part of any course in advanced plant physiology or in plant biochemistry.

A. T. JAGENDORF

ADVANCES IN CARBOHYDRATE CHEMISTRY. *Volume 15. Editor, Melville L. Wolfrom; assoc. ed., R. Stuart Tipson. Academic Press, New York and London.* $14.00. xii + 445 pp.; ill. 1961.

Volume 15 contains 9 chapters written by specialists in their respective areas of carbohydrate chemistry and biochemistry. The treatment is as consistent throughout as can reasonably be expected, and as up to date as the hazards of publication allow in this period of rapid advances. A good balance in the manner of dealing with the subjects is maintained, which is in sufficient detail to benefit the specialist, and comprehensive enough to be of interest to the nonspecialist.

During the last 2 decades there has been increasing interest in biochemical mechanisms of organic compounds in living cells. The enzymatic systems and the energies involved in the interconversion and synthesis of naturally occurring compounds have been intensively studied. This trend is reflected in Volume 15. The volume is therefore perhaps of greater interest to the biochemist than to the chemist, who is primarily concerned with the structure and chemical reactions of compounds. Only the first 4 chapters fall into the latter category.

The first chapter, Constitution and Physicochemical Properties of Carbohydrates, by B. Capon and W. G. Overend, is a treatment of physicochemical measurements of a range of sugars in terms of modern theoretical ideas. A physicochemical property is considered by the authors to be one which has been measured quantitatively. Examples of such properties are: density, solubility, spectra, and equilibrium constants.

In the second chapter, Methods in Structural Polysaccharide Chemistry, H. O. Bouveng and B. Lindberg point out that structural investigations of polysaccharides from natural sources do not lead, in most cases, to an assignment of a complete and generally acceptable chemical structure, because there are always uncertainties as to the finer structural details. This article is a review of the newer and more refined methods used in polysaccharide chemistry. The presentation is restricted to neutral polysaccharides and those containing uronic acid residues.

In Carbonates and Thiocarbonates of Carbohydrates, L. Hough, J. E. Priddle, and R. S. Theobald review the chemistry and the rather complex nomenclature of the sugar carbonate and the thiocarbonate esters, and indicate that these esters might well be used more extensively as "blocking groups" in synthetic efforts.

An extensive tabulation of the amino sugars and their derivatives is made by D. Horton in Tables of Properties of 2-Amino-2-deoxy Sugars and their Derivatives. This contribution is a modernized replacement of the one in Volume 7 and serves as an appendix to the chapter on Aspects of the Chemistry of the Amino Sugars, by A. B. Foster and D. Horton, in the preceding volume of this series.

In the chapter, Bacterial Nucleosides and Nucleotides, J. Jonsen and S. Laland summarize the present knowledge of this subject. This review deals with the nucleosides and low-molecular nucleotides isolated from bacterial systems and their structure and function in synthetic processes. The authors point out that the structure and metabolic function of bacterial nucleotides very often find their counterparts in the cells of higher organisms.

Another chapter dealing with the carbohydrate components in bacteria, entitled Polysaccharides of Gram-negative Bacteria, is presented by D. A. Davis. The author states that more than 20 different monosaccharide units are known to occur in bacterial polysaccharides, and 5 or more different kinds may be present in the same polymer. Since chemical aspects of the subject as a whole have become too extensive for a comprehensive review, he considers the products of Gram-negative species only; but in order to provide access to information about other microbial polysaccharides, he gives a comprehensive list of references to various reviews on this subject that have appeared since 1944.

In his review, The Biosynthesis of Aromatic Compounds from D-Glucose, D. B. Sprinson is primarily concerned with the various aspects of formation of shikimate and with its conversion to aromatic amino acids. Although the role of D-glucose is stressed, the author points out that the starting materials for the other known pathways may also be derived ultimately from D-glucose.

In his article, Dextran: Structure and Synthesis, W. B. Neely brings up to date the structural aspects of this polysaccharide, reviewed by Evans and Hibbert in Volume 2 of this series. In addition to describing the structural characteristics of dextran, the author includes a discussion of its enzymatic synthesis.

The last chapter, Chitin, by A. B. Foster and J. M. Webber, represents a comprehensive account of the chemistry and biochemistry of this important polysaccharide.

The volume also contains an obituary of the late Emil Heuser, a noted carbohydrate chemist primarily interested in the chemistry of cellulose. The biographer, L. E. Wise, eloquently characterizes Heuser, who, in addition to having been an excellent scientist, was also a "cultured European, an aristocrat with an ingrained love for music, drama, poetry, and for all forms of beauty." The reviewer, who had the pleasure of knowing Dr. Heuser personally, thoroughly agrees with the biographer.

In addition to the author and subject indices, Volume 15 contains a cumulative author index for Volumes 1–15.

W. Z. HASSID

THE CARBOHYDRATES. *The Chemistry of Natural Products. Volume V.*

By S. F. Dyke. Interscience Publishers, New York and London. $4.75. x + 232 pp.; ill. 1960.

Similar to the book entitled *An Introduction to the Chemistry of Carbohydrates*, by John Honeyman, that appeared in 1948, and to *Structural Carbohydrate Chemistry*, by E. G. V. Percival, published in 1950, Pyke's book is a compact and up-to-date account of the chemistry of a selected number of carbohydrates. While the former two books do not require the reader to have any knowledge of that branch of organic chemistry, requiring only a familiarity with the elements of aliphatic and aromatic chemistry, the present volume is presented on a more advanced level. For a full appreciation, some knowledge of structural carbohydrate chemistry would be needed.

The basic classical principles of the carbohydrates commonly treated in most textbooks are briefly presented. But the author quickly passes on to the more advanced and modern phases. The application of periodate oxidation, that served so well to elucidate many of the hitherto unknown structures of already known and newly synthesized and natural carbohy-

drates, is emphasized. Considerable attention is paid to the subject of Conformational Analysis, dealing with the *cis* (boat) and *trans* (chair) forms of the sugars whether they exist in free or combined form. It is pointed out that the sugars and their derivatives exist in solution as well as in solid state in various forms either in chair or boat conformations. The author briefly mentions the various methods, such as X-ray diffraction, nuclear magnetic resonance spectra, and infrared spectra, used as tools for conformational analysis. He also enumerates certain rules that serve as a guide to the prediction of the conformations of a particular sugar.

The author discusses some of the less common naturally occurring sugars. With the progress made in structural investigations of cardiac glycosides and antibiotics, some unusual sugars have been discovered. Among these branched-chain and deoxy sugars, the following have been found: apiose [(3-C-hydroxymethyl)-D-*glycero*-tetrose], cordiceptose [(3-deoxy-3-C-(hydroxymethyl)-D-*glycero*-tetrose], streptose [5-deoxy-3-C-formyl-L-xylose], hammamelose [2-C-(hydroxymethyl)-D-ribose], mycarose [2,6-deoxy-3-C-methyl hexose], and cladinose [2,6-deoxy-3-C-methyl-3-O-methyl hexose].

A brief description of the application of chromatography and its contribution to the advances of structural carbohydrate chemistry is included.

Each chapter contains a limited number of well-selected references to reviews and to the more recent original literature pertaining to the particular subject.

Throughout the book the author strictly adheres to the standardized carbohydrate nomenclature adopted by the American and British joint committees devoted to that task.

The compounds and the reactions are well illustrated with the Haworth perspective formulas. However, they represent a reproduction of small, handwritten formulas, which are difficult to read and which considerably detract from the appearance and usefulness of the book.

It is inevitable in writing on such a complex subject as carbohydrates, that some inaccuracies creep in. The author gives values for the molecular weights for starch and glycogen of about half a million for the former and over one million for the latter. Recent work has established the molecular weight of these polymers as of a factor greater by about ten. In discussing the molecular structure of starch, the author presents a choice between Haworth's laminated and K. H. Meyer's multibranched structure. Actually, Meyer's multibranched structure for starch has long been accepted as the correct structure.

The final chapter is devoted to carbohydrate metabolism, briefly covering glycolysis, photosynthesis, biosynthesis of monosaccharides, and polysaccharides. The metabolic processes are illustrated by many charts representing various pathways. As expected, it would be difficult to present adequately such a vast subject in a few pages. As a result, many inaccurate and misleading statements are encountered. As an example, on p. 214 the synthesis of sucrose in plants is given by a reaction between uridine diphosphate glucose and D-fructose-1-phosphate. Actually the reaction takes place between this sugar nucleotide and D-fructose-6-phosphate.

The various charts showing the metabolic pathways invariably contain many phosphorylated sugars, the chemistry of which is not even mentioned in this book. It would be preferable to omit this chapter completely, because very little could be derived by the reader who is not acquainted with the field, and certainly it will prove of very little use to a biochemist who knows the subject.

As a short book on structural carbohydrate chemistry, this work represents a useful addition to the literature on the subject.

W. Z. Hassid

MICROBIOLOGY

PERSPECTIVES IN VIROLOGY. *Volume II. The Gustav Stern Symposium.*

Edited by Morris Pollard. Burgess Publishing Company, Minneapolis. $8.00. x + 220 pp.; ill. 1961.

This second Gustav Stern Symposium has as its focal point the tumor viruses, although about half of the papers depart from this central theme. The symposium is dedicated to Peyton Rous, who some 50 years ago demonstrated the filterability of the fowl sarcoma agent and since then has been a leading contributor to studies of virus-induced tumors. A summary, by T. M. Sonneborn, of some aspects of hereditary infections by *kappa* particles, and the general lessons this unique system may have for considerations of other host-parasite systems, leads off the discussion. The areas of electron microscopy, biochemical changes in infected cells, and criteria for virus identification are discussed in several articles, mainly with regard to human and chicken tumor viruses and adenovirus. Two additional articles discuss reproduction of polio virus and a third, by A. Isaacs, reviews the properties of interferon. Just as masterful as his concluding paper in the first volume of *Perspectives* is his epilogue for this second volume: Integrative and Creative Aspects of Infection, by R. J. Dubos.

Philip E. Hartman

AN INTRODUCTION TO THE BIOLOGY OF MICRO-ORGANISMS.

By Lilian E. Hawker, A. H. Linton, B. F. Folkes, and M. J. Carlile. St. Martin's Press, New York. $6.75. viii + 452 pp. + 40 pl.; text ill. 1961.

Another gap has been filled in the field of microbiological texts. The authors have done an excellent job of preparing an introduction to the morphology, physiology, and ecology of *all* of the major groups of microorganisms. The book is well-written, well-illustrated, and modestly priced. The fundamentals of bacteriology, mycology, protozoology, algology, and microbial physiology have been condensed into a single volume. This is just what we need—or is it?

As the authors point out, "university courses in microbiology and text-books dealing with the subject are often concerned almost entirely with bacteria, and even with the comparatively small number of those which cause disease, and contain only scanty and unsatisfactory references to the other important groups of micro-organisms." In this volume the authors have solved the problem of breadth: the book contains information regarding the fungi, protozoa, and algae not found in other texts of general microbiology. Another problem, however, arises: one of depth. Anything added to a course in bacteriology must be a replacement, rather than a supplement. Something important must be omitted in order to accommodate another important item. Whether or not this volume will satisfy the needs of the reader depends upon his relative sense of values, as far as subject matter is concerned. In addition, use of this type of text is based on the assumption that the student has an exceptional background in biology and chemistry, or that he will develop one quickly as the course proceeds. This assumption arises because many points are, of necessity, covered superficially in the text. For example, only 1 page (p. 29) is devoted to explaining the various modes of recombination in bacteria, only 1 page (p. 142) is used in describing the multiplication of bacteriophage, in 20 pages (pp. 188–208) the reader is given the entire gauntlet of reaction pathways in metabolism, and 5 lines (p. 406) are used to tell about the microbial transformation of steroids. Thus, the reader must rely heavily on outside sources for more detailed explanation of various phenomena, if any understanding and appreciation of the material is to be gained. Fortunately, the authors have anticipated this problem, and have incorporated a list of very well-chosen books and articles for reference and further study following each chapter. The assignment has thus been made: attend the lecture, read the book, make liberal use of the outside sources suggested, and learn something. This introduces a philosophy of education whereby if the student performs well we can credit our lectures and the text, but if a poor showing is made the student receives the blame for not pursuing the subject sufficiently on his own. On the other hand, no claim can be made that the student using this text has been 'spoon-fed' his general bacteriology. Regardless of the approach, the good students will probably be successful and the poor students will not. In which manner do you wish to stimulate or discourage your students?

PAUL A. HARTMAN

PRINCIPLES OF MICROBIOLOGY. *Second Edition. By Walter W. Krueger and Karl R. Johansson. W. B. Saunders Company, Philadelphia and London.* $6.75. xxiv + 563 pp.; ill. 1959.

The authors of this second edition have succeeded in presenting succinctly to the undergraduate student the various disciplines of microbiology in "palatable" form. It is extremely well-written and attempts have been made to bring the subject matter up to date. At the end of each chapter there is a question section which should prove a useful guide to the student in determining whether he comprehends the subject matter, and orients him as to the importance of certain points. In addition, there are selected references which can be employed by the interested student to further his understanding of the subject matter. The section on physiology of microorganisms has been written in such a way that students with even a limited background in chemistry and biology can comprehend the material. This book is highly recommended for an introductory course in microbiology.

MORTON M. WEBER

LABORATORY MANUAL FOR GENERAL MICROBIOLOGY. *By Jay V. Beck, Don H. Larsen, David M. Donaldson, and Richard D. Sagers. Burgess Publishing Company, Minneapolis.* $2.00 (paper). viii + 56 pp.; ill. 1961.

HEALTH AND DISEASE

THE METABOLIC BASIS OF INHERITED DISEASE. *Edited by John B. Stanbury, James B. Wyngaarden, and Donald S. Frederickson. McGraw-Hill Book Company, New York, Toronto, and London.* $30.00. xiv + 1477 pp.; ill. 1960.

Tradition has it that structure precedes function. This is reflected in medical school curricula, in which the neophyte's introduction to medicine involves dissection of a lifeless human remnant. This is followed or accompanied by histology and neuroanatomy, sometimes with only passing reference to the origin of the organs, what their functions might be, and how they carry them out. Later, the classical introduction to disease consists of examination of inanimate tissues whose altered and distorted structures can only suggest the changes in their capabilities to carry out their allotted purposes.

But medical teaching is just now in the midst of revolution. Much is known about sub-cellular organization and localization of elements whose roles in the economy of the cell can be characterized by chemical and biophysical techniques. Increasingly, morphology is deemphasized and function is stressed. Cell metabolism is described in terms of its component molecules and whether these molecules are engaged in providing the matrix in which cell business is transacted, or in providing the wherewithal to complete the business is not of primary importance. Of key importance is comprehension of the design and construction, both normal and abnormal, of these molecules, and the aim of medical science, no less than that of general biology, is directed to this understanding. The ultimate determinant of molecular architecture and function is the genetic material, so that all cell activities (normal and abnormal) are directly or indirectly under its control. Recognition of health and disease in these terms has meant that genetics is taking its place as a relevant discipline in medical teaching.

We are all very much in the debt of the editors and authors of this book, since they have summarized the available material on the genetic control of abnormal metabolism in man. That the book is enormous attests to the usefulness of man as an object for the study of these aspects of gene action. No one person could be equally knowledgeable in all the fields covered, so the editors have wisely chosen authors whose special experiences make them expert. There are in all 11 "Parts," including 46 chapters. To each chapter is appended a list of references which for the whole book total 5,098. This number reflects the thorough treatment each author has given his subject. The 11 parts of the book divide the chapters into related groups, e.g., disorders of carbohydrate metabolism, lipids, amino acids, etc. These categories are, of course, useful and are necessarily pragmatic and arbitrary. They reflect the salient aspect of each disease with the implication that that particular feature is the most basic one currently known and most nearly proximal to the gene action. In many instances, such a designation necessarily reveals our ignorance of the nature of the aberrant mechanism; for example, "diseases manifest primarily in renal tubular transport." It is to be hoped that this book will go through several editions (though in the course of these it may become a multivolume "handbook"); and as it does, it will be interesting to see the rearrangement of the chapters and divisions as investigations provide new insight into gene action. Perhaps some of the above-mentioned disorders will turn up under disease of, for example, carbohydrate metabolism or of some new category specifying a lesion at a more fundamental level.

The chapters have a nearly uniform arrangement. Normal metabolism is reviewed, some attention is given to the clinical manifestations of the disorder in question, the abnormal metabolism is exhaustively treated, and finally evidence favoring genetic determination is given and mode of inheritance is discussed. It should be stated that this is not a textbook of genetics, but that its content fulfills exactly the promise of its title; that is, it deals with the chemical attributes of disorders which are genetically determined. The editors have set a high standard. All of the chapters are not of equal quality, but none is inadequate, and some are of absolutely first quality. To single out any particular ones probably reflects the biases of the reviewer, but I cannot resist special notice of the chapters on Vasopressin-resistant Diabetes Insipidus, Cystinuria, and Gout. I do not think of anything germane which has been left out, and applaud the editors' inclusion of such conditions as Xanthinuria and Orotic Aciduria. For these there is no evidence of genetic origin, but their characteristics are such as to suggest that time will bring it. In sum, this is an excellent and most useful book. I hope its price will not preclude its wide dissemination.

BARTON CHILDS

MEDICINE AND ANTHROPOLOGY. *Lectures to the Laity, No. XXI. N. Y. Acad. Med. Edited by Iago Galdston. International Universities Press, New York.* $3.00. 165 pp.; ill. 1959.

An Introduction by the editor is followed by these contributions: Man, Magic and Medicine (Paul Fejos); The Humanist Looks at the Doctor (John W. Dodds); The Ecology of Health (Marston Bates); Cultural Mentalities and Medical Science (F. S. C. Northrop); Mental Illness and Acculturation (Alexander H. Leighton); and Acculturation in Relation to Concepts of Health and Disease (Raymond Firth).

This small volume contains much stimulating insight and wise comment. The topics differ with contributor; strictly speaking, there is not a single thread of objective running throughout the volume. There is, however, a frequently expressed conviction to the effect that men in different cultures are not wholly dissimilar in fundamental personality traits relevant to the physician's task. Account must be taken of the culture background of the patient; there is no physical ailment that does not have repercussions in the psyche. There are pungent illustrations of these principles. Fejos indicates that so-called civilized man has perhaps as many "superstitions," beliefs accepted without validation, as has tribal man and the folk in Western culture. Leighton details experience with Eskimo on St. Lawrence Island, off Alaska. Bates calls attention to man's tendency to kill, in war, members of his own species, for which tendency he suggests the word anthropoktony—"from *anthrops*, man, and

ktonos, to kill." The explanation of this tendency, he believes, is to be found in territorialism. Northrop emphasizes the strains on personality produced by culture change.

WILSON D. WALLIS

ESSENTIAL TREMOR. *A Clinical and Genetic Population Study. Acta psychiat. scand., Supp. 144, Vol. 36. By Tage Larsson and Torsten Sjögren; with the assistance of Göta Petersson. Ejnar Munksgaard, Copenhagen.* (paper). 175 pp. + 1 folded chart. 1960.

The authors assembled 210 cases of hereditary essential tremor in one parish of Sweden. The age of onset was on the average about 50 years and was somewhat later for females than for males. The age of onset showed high intrafamilial correlation. "Anticipation" was not observed. Fine rapid tremor of the hands is usually the first symptom. Tremor of the arms, tongue (with dysarthria), head, legs, and trunk develops later, usually in the order listed. Mild extrapyramidal symptoms in the form of rigidity and stiffness of gait occurred frequently, but the clinical picture was easily distinguished from Parkinsonism. Mental deterioration was not a feature. With 2 exceptions all 210 cases could be traced back to 4 ancestral couples. The inheritance was autosomal dominant. From observation of about 15 presumed homozygous individuals it was concluded that there is no difference from the disease in heterozygotes. It was estimated that more than 9 per cent of males and 6–6.5 per cent of females of the parish carry the gene for essential tremor. The authors could find no reason to suspect selective fertility, selective mortality, or assortative mating as factors in the high gene frequency observed. Rather, chance variations occurring when the population was small—about 150 persons in the late 1700's—seem to have been responsible.

VICTOR A. MCKUSICK

CIBA FOUNDATION TENTH ANNIVERSARY SYMPOSIUM ON SIGNIFICANT TRENDS IN MEDICAL RESEARCH.

Edited by G. E. W. Wolstenholme, Cecilia M. O'Connor, and Maeve O'Connor. Little, Brown and Company, Boston. $9.50. xii + 336 pp.; ill. 1959.

This review not only aims at selecting significant trends, but also marks 10 years of the unique Ciba Symposia. Since the rate of accumulation of new knowledge now exceeds the rate of assimilation, the symposium (from the Greek meaning "fellow drinkers") has become an essential device in the formulation of new theories and in the use of new data. The Ciba Symposia, by careful selection of both topics and participants, have established a model forum for the exchange of ideas. The custom of publishing expertly edited manuscripts *and* remarks has allowed the reading public to listen in on the original exchange.

For the tenth anniversary, the editors and trustees have opened the Symposium with molecular biology and ended with an essay on the dimensions of contemporary U. S. medical research. In between are samplings of current research on subjects which range from whole populations to pyridine nucleotides. The sampling process necessarily delimits whole disciplines from consideration, and some which have been left out may question the equity of the choices. There is, for example, nothing on the ultrastructure of cells, which seems strange when the electron microscope within this very decade has brought about a revolution in morphological knowledge quite as great as that originally wrought by the light microscope.

The tremendous expansion of research facilities has raised the age-old question of how progress is actually made. Each essay here by a man who has been part of the process stimulates ideas. Burnet's emphasizes that the idea is the thing. His brief essay on population dynamics of cells and the importance of mutants combined with clonal selection develops this. On the other hand, Pickering's emphasis on the problem of differentiating essential hypertension sharply from the general aspect of increasing blood pressure with age, and the many factors influencing it, brings out the need for constantly rechecking and re-examining our ideas with good quantitative data at hand. Both approaches are obviously interdependent.

The Symposia are stimulating, provocative, and instructive. Since they are by nature also temporary, we wonder whether they could not serve a wider audience if paperbound (and priced) like Penguins, Pelicans, or Puffins. How about a Ciba Phoenix?

FREDERIK B. BANG

PSYCHOLOGY AND ANIMAL BEHAVIOR

THE CENTRAL NERVOUS SYSTEM AND BEHAVIOR. *Translations from the Russian Medical Literature. Collected for the Participants of the Third Macy Conference on the Central Nervous System and Behavior, held under the Joint Sponsorship of The Josiah Macy, Jr. Foundation and the National Science Foundation, Princeton, New Jersey, Feb. 21–24, 1960. Russian Scientific Translation Program, National Institutes of Health, Bethesda.* x + 1051 pp.; ill. 1960.

As stated in the Preface by Frank Fremont-Smith, the selected translations were prepared primarily for the critical review of the participants at the Third Macy Conference. The selection of 70 articles was culled largely, as might be expected, from cur-

rent Soviet research in Pavlovian physiology and psychology—that is, classical conditioning and closely related phenomena—as published in such periodicals as *The Pavlov Journal of Higher Nervous Activity* (available in English since 1958), *Works of the Institute of Higher Nervous Activity*, *The Sechenov Physiological Journal of the USSR* (available in English since 1956), *Material on Evolutionary Physiology*, *Problems of Psychology*, and several others. However, one finds in the collections also a number of general philosophical articles translated from *Problems of Philosophy*, on Determinism and teleology. Materialist theory of reflection and the theory of development of living matter, and Philosophical problems in contemporary genetics. And there are also articles of a general biological as well as of a specific anatomic nature, e.g., The role of physics and chemistry in the investigation of biological problems; Genetics of micro-organisms and present-day views on heredity; Topography of proteins in the central nervous system; Histochemistry of brain phosphatase in rabbits during ontogenesis; and Development of area 17 of the cerebral cortex in humans during the second half of intrauterine life.

Few of the translations are free from confusing literalness of rendition and from occasional errors which, combined with the not uncommon inadequate reportage in the original Russian, make no doubt the first reading of the articles a difficult and really annoying experience. Yet, second and third readings with some imagination and will power will be highly rewarding and profitable. Soviet research contribution in the area is highly significant.

GREGORY RAZRAN

THE MIND OF MAN. *A History of Psychotherapy and Psychoanalysis.*

By Walter Bromberg. Harper Torchbooks, Harper & Brothers, New York. $1.95 (paper). xxiv + 344 pp.; ill. 1959. (Reprint of 1954 edition then entitled: *Man Above Humanity: A History of Psychotherapy*. New 7 page preface.)

CURRENT PROBLEMS IN ANIMAL BEHAVIOR.

Edited by W. H. Thorpe and O. L. Zangwill. Cambridge University Press, New York and London. $8.50. xvi + 424 pp. + 2 pl.; text ill. 1961.

This volume of essays is the outcome of the activities of a small group of Cambridge scientists interested in problems of behavior in animals and man. One of its objects is to bridge the gap which has hitherto divided the ethological and psychological approaches to the study of behavior. The book is divided into 4 parts: Neural Mechanisms and Behaviour, Experimental Studies of Animal Behaviour, Studies of Problems Common to the Psychology of Animals and Men, and Theoretical Approaches to Behaviour. The editors have provided short introductions to each section. It is not possible to outline in detail all the specific topics touched in the 14 papers comprising the volume. Suffice it to say that all are of high quality. It is a tribute to the sponsoring university that such a comprehensive attack on the problem of animal behavior could be mounted within a single institution. Although it is regrettable that such a delay occurred between the time these discussions were prepared and their appearance in print, since some points are already out of date, this is, nevertheless, a learned and valuable volume. It must be read by any worker seriously interested in animal behavior. It reveals a great deal about animal behavior, not only that of the animals discussed but also of the discussants themselves.

VINCENT G. DETHIER

HUMAN BIOLOGY

RACE AND SCIENCE. *The Race Question in Modern Science. Specific Analysis from UNESCO.*

Columbia University Press, New York. $5.00. 506 pp. 1961.

Race and Science is a re-issue (in more elegant and sturdy format) of a UNESCO-sponsored volume that first appeared in 1951 under the title *The Race Question in Modern Science*. It is the greatest compliment to its contributors that their apparently unaltered essays scarcely stand in need of alteration. While the price of the book has increased, it is still surprisingly low. Indeed the only faults seem to be a slightly eccentric division of the essays into three groups; a regrettable absence of bibliographies to the essays by Klineberg and Rose; and an unequal effort by the other contributors in bringing their bibliographies up to date, or including foreign-language items.

While 4 printings in 10 years is evidence enough of a steady demand, one could wish an even wider use of this remarkable book. Dunn, Morant, and Shapiro provide excellent discussions of the physical, and Klineberg and Jahoda of the mental, factors involved in the concept of race. Comas, Leiris, and Levi-Strauss survey the cultural dimensions of race distinction. Little and Rose explore the relevance of social context to racial notions; and a second contribution by Shapiro gathers numerous approaches into a study of a single group: the Jews. Taken with a short account of human paleontology, the book could thus serve the needs of physical anthropology courses far better than most textbooks now in college use.

But much more than this, the contributors are an unusually varied sample of intellectual preoccupation, analytical method, style of exposition, and scholarly background. Their essays are not only

scientifically reputable but highly literate. In presenting a rounded discussion of the problem of 'race,' they have also given the reader a guided tour of the intellectual process, the method of scholarship, and the art of intelligible communication. It can profitably be read (and at the price, owned) by anyone who cares—or claims—to be 'educated.'

NEVILLE DYSON-HUDSON

RACES OF MANKIND. *Their Origin and Migration. By Calvin Kephart. Philosophical Library, New York.* $6.00. xvi + 566 pp.; ill. 1960.

The jacket blurb says, "Apparently for the first time in history, the author has connected up all ancient tribes and nations of mankind filially.... He also explains the causes of racial differences." This may have been apparent to the publisher. It is not to the reviewer. In his preface Kephart warns against "captious attitudes of critics whose earlier knowledge of the subject may be disturbed." He does not disturb; he violates. He holds out for "pure" races, he maintains an "Aryan race," a "Hebrew race," and he asserts that "races remain substantially unchanged through long periods in the absence of intermarriage with dissimilar traits."

This book, to judge by references, is dated in its material and viewpoint. Kephart leans heavily upon the Book of Genesis, Diodorus, Herodotus, Homer, Pliny, Strabo, Tacitus, Thucydides, Xenophon, the 13th edition of the Encyclopedia Britannica, a handful of nineteenth century books, and a smattering of twentieth century references. Missing are recent data on racial origins in terms of morphogenetic bases and physio-biochemical interpretation. In my opinion, this is another book in the vein of *The Passing of the Great Race*, by Madison Grant, only more so.

Kephart's use of racial terms presumes to denote origin. Thus, *Indafrican* or Black race is used, "since the Negro race developed in northern India." *Caucasian* and *Indo-European*, for the white race, are discarded in favor of *Aryan*, or Brown-White race, from Arii of ancient Persia, on the Arius River. The Aryans, he says, early reached the Mediterranean area, for certain Paleolithic "Galilee" men were of this type. The Cro-Magnards were "the first division of Aryans that revealed itself in Europe"; incidentally, they had "superior brain power and closely observant and creative minds." The Nordics, who originated in an Indonesian stock, are Aryans from the upper reaches of the Indus River in western Tibet; they went into Europe via the Karakoram Pass. A further sally into origins suggests that "the Red and White subraces were not such originally but were derived from the Yellow and Brown races, respectively...."

The author goes in heavily for a biobehavioral slant, speaking of "the racial soul or mind of each branch of the human stock." Modern Jewish peoples have little in common with ancient Hebrews "except a peculiar type of psychology, some traces of the Kassite or Hittite physiognomy, and their religious and other social customs." The African Negro is quoted as having "in his natural environment" a brain that is similar to that of a "western European who has had the frontal lobes of his brain disconnected (or like a 'constitutional psychopath')." Kephart cites Prime Minister Verwoerd of the Union of South Africa on the cultural capabilities of the African native, which is about like quoting Khrushchev on the merits of capitalism. It is not likely that the Negro, anywhere, he avers, has a future of "intelligent participation in a democratic electorate." The same old theme of race-mixture and its "retrogressive effects on the higher race" is stressed.

It is not necessary to go much further. This is not a scientific book despite its heckling by innumerable quotes, references and opinions, from "authorities" of a bygone age. It is not an objective book. Kephart is using the "hard sell" for the Aryans and misses no chance to upgrade them and downgrade other groups. It is not race that is central in Kephart's thinking; it is racism of the rankest sort that will appeal only to those who would assume a role of white superiority and potentiality. If the publishers had referred the manuscript to the evaluation of competent anthropologists, it would have ended in the wastebasket.

WILTON MARION KROGMAN

BIENNIAL REVIEW OF ANTHROPOLOGY 1959. *Edited by Bernard J. Siegel. Stanford University Press, Stanford.* $6.00. x + 273 pp. 1960.

This collaboration includes the following contributions: Recent Advances in Physical Anthropology (Gabriel W. Lasker); Cultural Change (Louise S. and George D. Spindler); Psychocultural Studies (John J. Honigmann); Social Organization (Harry Basehart); Recent Trends in Soviet Anthropology (Lawrence Krader); Language (Floyd Lounsbury); and Political Anthropology (David Easton). In the main, the period of publications cited is from 1955–1958, inclusive. The extent of the coverage is illustrated by the fact that Lasker cites 412 sources; the Spindlers, 132; Honigmann, 407; Basehart, 121; Krader, 123; Lounsbury, 234; Easton, 25 and several abstracts. There is an excellent index (in which Anauk *should* read Anuak).

Some contributors have successfully combined the essay form with a detailing of the problems treated, or findings recorded, in cited sources. Easton deals

at some length with the problem of identifying and defining government and political behavior in simple cultures that have no obvious machinery of government. Lasker remarks, with regard to physical anthropology in the period from 1955 through 1957: "it seems that on the whole the works under review—perhaps more than those of an earlier two-year period—are directed to specific anthropological problems rather than to the study of a particular period or geographic region. These problems, if they continue to interest scholars, presage trends in findings; and the accomplishments of physical anthropology today project in greater relief the questions that remain to be answered tomorrow." His cited sources, it appears, justify this inference. They include, however, concern with the processes of human evolution—inbreeding, genetics, physiographic influences, new discoveries of fossils, and the interpretation of the fossil record; chemical anthropology; growth, body type, and composition; and nutrition.

WILSON D. WALLIS

DISCUSSIONS ON CHILD DEVELOPMENT. *Proceedings of the Fourth Meeting of the World Health Organization Study Group on the Psychobiological Development of the Child, Geneva, 1956. Volume 4.* *Edited by J. M. Tanner and Bärbel Inhelder. International Universities Press, New York.* $5.00. xiv + 186 pp.; ill. 1960.

This volume reports the proceedings of the last of four annual meetings on child development. The preface warns the reader that a reading of the first three reports is essential to an understanding of the present volume. Among the participants in the discussion were J. Piaget, B. Inhelder, Margaret Mead, K. Lorenz, W. Grey Walter, E. Erikson, R. Zazzo, and John Bowlby. The reviewer has always felt that discussions of this sort are of great benefit to the participants but of less benefit to a reader of the proceedings. This may in part be because they tend to reach a stage where everyone is congratulating everyone else on how wonderfully mutual understanding has flourished: this invariably occurs just at a point where the reader has concluded that all is confusion. The reader always wants to interrupt rudely and cannot. In this particular discussion I myself wanted to interrupt the flow of agreement between Piaget (speaking for Piaget) and Bowlby (speaking for psychoanalysis) and ask whether the suddenly revealed harmony between Piaget and psychoanalysis might not tell us more about Bowlby's view of psychoanalysis than anything else. The harmony seems to result from Bowlby's softening of classical analytic views and even from his apparent inability to pronounce the shibboleth of psychoanalysis. Each reader of this stimulating book will have the pleasure of noting points where he would like to interrupt, which is, after all, the real justification for publishing these discussions.

PAUL CRANEFIELD

THE PROCESSES OF ONGOING HUMAN EVOLUTION. *Edited by Gabriel W. Lasker. Wayne State University Press, Detroit.* $3.75. iv + 108 pp; ill. 1960.

The formal proceedings of a meeting of the American Anthropological Association (1959) are presented here as 6 essays. All are concerned with factors which influence, presumably at the present time, generation-to-generation evolution in man, in situations which are relatively restricted in both space and time. The reviewer agrees with the editor that this symposium is indeed an appropriate and useful means of celebrating the Darwin centennial year.

The following essays are included: Climate, Culture and Evolution (P. R. Baker); Natural Selection, Disease and Ongoing Human Evolution, as illustrated by the ABO Blood Groups (F. B. Livingstone); Metabolic Polymorphisms and the Role of Infectious Diseases in Human Evolution (A. G. Motulsky); Adaptation, Selection and Plasticity in Ongoing Human Evolution (F. S. Hulse); Migration, Isolation, and Ongoing Human Evolution (G. W. Lasker); and Irradiation and Human Evolution (E. W. Reynolds).

The evolutionary forces (drift, selection, migration, mutation) which tend to alter gene frequencies are considered in terms of their probable effects on the phenotypic constitution of present and near-future human populations, as well, of course, as those selective agents (viz., infectious disease) which have very likely contributed strongly to the present genetic structure of human populations. Anthropologists and geneticists will find these essays of considerable interest, particularly as they indicate the common problems and lines of analysis of these two fields, upon whose cooperation and mutual understanding the effective exploitation of evolutionary theory as it pertains to man so strongly depends.

WILLIAM J. YOUNG

THE CONTENT AND STYLE OF AN ORAL LITERATURE. *By Melville Jacobs. Wenner-Gren Foundation for Anthropological Research, New York.* $5.00 (paper). viii + 285 pp. 1959.

Jacobs, a linguist and an Americanist, has recorded, translated, and analyzed eight stories told by Clackamas Chinook, an Oregon tribe. These were obtained from one of the last two (or three) speakers of that dialect.

There is an analysis of the literature as a whole, including tables not published here, and a pointing

up of traits of the contents: emphases; personality traits of men, women, and children, depicted or implied; humor; the concept of the good; the world view; included songs. There are practically no existing records of the aboriginal culture.

The author reconstructs much of the culture on the basis of these stories. This procedure will appeal to some; some will consider it more hazardous than entertaining, for, as indicated by the author, it cannot be validated.

Whether oral literature is more adequate for this purpose than is written literature for a literate culture is a moot point. A few gratuitous assumptions must be made before one can accept the author's interpretations as a reflection of reality.

WILSON D. WALLIS

HUMAN EVOLUTION. *Readings in Physical Anthropology.*

Edited by Noël Korn and Harry Reece Smith. Henry Holt and Company, New York. $5.50. xvi + 447 pp.; ill. 1959.

It is common, and seems reasonable, to assume that a reader will contain important source material extracted from original publications which may, in all but the best-endowed libraries, be very difficult of access. If the jacket describes the book as "accomplishing in ... readings what might be done in a good single text," one further assumes that someone has undertaken the admittedly difficult task of collating the significant original contributions on which the current presuppositions of physical anthropology are ultimately based.

Unfortunately this reader presents nothing of the kind. Only 3 of its 40 chapters are drawn from professional journals, and only 1 of these from the *American Journal of Physical Anthropology*, which one would have thought to be a prime source for a reader in the subject. Half the book (21 chapters) is taken from previous texts on physical anthropology, general anthropology, and the biological sciences: 5 chapters from *Fossil Men*, 4 from *Up from the Ape*, 3 from *Mankind So Far*, and so on. These are supplemented by chapters taken from *Scientific Monthly* (4), *Scientific American* (6), and other sources. All are connected by brief editorial matter.

The authors' students are fortunate in their teachers' evident appreciation of the multifarious elements of physical anthropology and of its lively presentation. Some of the selections are very neat, and it is good to have them reproduced: the Dunn's brief survey of a field problem in the Jewish community at Rome, or Simpson's elegant survey of general theories of evolution, for instance. But to present snippets of typical course reading as a self-contained volume is something else again, and in this respect the reader must be considered a dubious enterprise. In length the text could be considered as suitable for advanced students, for one would hardly inflict over 400 pages of physical anthropology on freshmen. But in its largely text-derived or predigested content it is not for advanced students, despite brief treatment of DNA, the amniote egg, etc. The lack of impact that perhaps inevitably accompanies second- and third-hand reporting is an additional disability for advanced reading: why not, for example, a geologist instead of an anthropologist (however good) for a general survey of the Pleistocene, or a more direct source for Bergman's rule, if it is to be discussed? None of this is to quarrel with the competence with which various subjects are discussed in the book, nor with an editor's necessary right to anthrologise in terms of his own understanding and personal preference. But it *is* to enter a plea for the recognition that texts and readers are valid in different domains, can hardly replace each other, and are very likely to be sterile if hybridised.

It may be that available textbooks on physical anthropology (some of which are very good) are not adequate for all needs: but surely this is an invitation to write a new text with a distinctive bias. It is certainly true that readers in physical anthropology would be helpful; but surely it would be more profitable and exciting to build them primarily from the professional journals, and those goldmines, the Wenner-Gren yearbooks of physical anthropology, than from predigested surveys written (however elegantly) for other audiences. And whatever strategy is adopted, surely one must stop short of cannibalising textbooks to produce other textbooks, for this is to imply that further original effort can, essentially, be dispensed with.

NEVILLE DYSON-HUDSON

AN ANTHROPOLOGICAL RECONNAISSANCE IN WEST PAKISTAN, *1955. With Appendixes on the Archaeology and Natural History of Baluchistan and Bahawalpur. Papers Peabody Mus., Vol. LII.*

By Henry Field. Peabody Museum, Cambridge. $9.75 (paper). xii + 332 pp. + 100 pl.; text ill. 1959.

In this latest of some half-dozen stout volumes contributed to the Peabody Museum series, Henry Field has extended his industrious reportage of the Middle East into Baluchistan. As the recent work of the brilliant young Norwegian anthropologist, Frederick Barth, has shown, this general area is one of the greatest fascination, and one urgently needing study. It is therefore all the more regrettable that the volume under review should appear to take us little farther forward in most respects than the sources on which it is largely based.

The subjects covered in the volume are topography, demography, local history, archaeology, physical

anthropology, ethnology, natural history, and bibliography. Most are given such episodic treatment that the total impression is of random jottings. Lists of various features—cephalic and nasal indices, rainfall, livestock numbers, plant specimens, for example—are scattered throughout.

The inclusion of the word *Reconnaissance* in the title must be allowed to disarm criticism to some extent; but a reconnaissance usually is made with some end in view, and what that is quite fails to appear. Again, there is accepted value in the collation of secondary sources where these are very difficult of access and some new and relevant synthesis is attempted; but no synthesis is achieved by the book, nor can most of its sources (largely printed) be considered inaccessible.

It seems a great pity that Field's evident industry, time, means, and capacity to command assistance should have been deployed with such disappointing result.

The quality of the numerous photographic plates is excellent.

NEVILLE DYSON-HUDSON

DIE ANTHROPOLOGIE DER KANTONE UND DER NATÜRLICHEN LANDSCHAFTEN. *II. A. Textband. B. Atlas. Anthropologia Helvetica. Arch Klaus-Stift., Ergänzungsband, Band XXXIV.*

By Otto Schlaginhaufen. Zürich. 708 pp.; (atlas) 8 pp. + maps. 1959.

In 1930 or thereabouts Schlaginhaufen began a survey of the physical anthropology of Switzerland. Now, 30 years and 30,000 young adult males later, comes this monumental contribution. In the Martin tradition this is a morphometric survey, with a few morphological features. There are 16 measurements: stature; sitting height; leg length; span; head length; head breadth; min. frontal diam.; morph. face height; bizyg. breadth; physiog. upper face height; mand. height; mand. breadth; inner canthic breadth; outer canthic breadth; nose height; and nose breadth. There are 18 indices: sitting height/stature; rel. span; rel. head length; rel. head breadth; cephalic, trans. fronto-parietal; rel. bizyg. breadth; rel. morph. face height; facial; physiog. upper face; fronto-zyg.; mand.-zyg.; trans cephalo-facial; inner-outer canthic; nasal; trans. naso-facial; sag. naso-facial; and nose breadth/face height. There are 4 descriptive traits: hair form, eye color, nasal profile, and occipital contour.

The selection of measurements and descriptive traits is of interest, more for its omissions than its inclusions. Skin color, head shape, and facial contour, as examples, are not given. Occipital contour is chosen, possibly for an Alpo-Dinaric contrast. There are no trunk or detailed limb measurements and no indices of trunk, limb/stature, or limb/limb ratios. As might be expected for a study begun 3 decades ago, there are no data on blood groups or other physiologico-biochemical variables. There are no genetic data, nor are there in the analysis any directly derived or expressed genetic implications. Nonetheless, there emerges a reasonably clear picture of Switzerland as an anthropological entity.

Schlaginhaufen has handled his data on a geographical or regional basis: 22 cantons, subdivided into 184 areas. Accordingly, the sample breakdown results in most series numbering less than 100, with many as small as 40. Many stated regional differences lose complete statistical significance in consequence. Despite this, the maps reveal smaller areal differences quite clearly; by contrast, larger regional units seem to be fairly similar in terms of their over-all dimensional and trait complexes. Some intriguing general results emerge: urban males are taller than rural; differences do not cleave to linguistic lines, i.e., there are no differences between German- and non-German-speaking peoples.

If the report be viewed in the light of current population genetics and social structuring, it makes a lot of sense. For example, in many cases adjacent areas (valleys) showed as many differences as did entire cantons. In terms of village endogamy, there is every reason to ascribe a finding such as this to microevolution and/or genetic drift. We are indebted to Schlaginhaufen and his associates for a magnificent contribution.

WILTON MARION KROGMAN

A HANDBOOK OF ANTHROPOMETRY.

By M. F. Ashley Montagu; with a section on The Measurement of Body Composition, by Josef Brožek. Charles C Thomas, Springfield. $5.00. xii + 196 pp.; ill. 1960.

This book is really the unchanged latter portion of Montagu's 1960 (3rd ed.) *Introduction to Physical Anthropology*. As such, it does not fully carry its own weight. The 29 pp. bibliography, for example, is out of place, for it refers to far more than mere measuring techniques.

There are 3 parts to this volume: Measurement of bones and body, by Montagu; The Measurement of body composition, by Josf Brožek; and papers on gene and genotypic equilibria, and ethnic group, by Montagu. The Unesco Statement on Race, which follows, is a *non sequitur* in an anthropometric handbook.

The sections on somatometry and osteometry are essentially in the Rudolph Martin tradition, but are very simply written, even carelessly at times (e.g., in measuring foot length, pternion and akropodion are reversed). What really worries one is that one doubts if a beginner, without a trained physical anthropologist at hand, could learn how to measure

accurately. Under *sitting heights* the measurement "sitting suprasternal height" goes "from the middle of the anterior-superior border of the manubrium sterni to the floor"; obviously, it should be to the plane of the "bench or box" upon which the subject is seated. In measuring the body or bones the student is not acquainted with absolute and relative variability and reliability. In tables of tooth eruption, as an example, only average ages are given. For permanent teeth Hurme's data, given mean and standard deviation, could well have been given. The data on suture closure are those of Todd and Lyon (1925); recent studies by Brooks, Singer, McKern and Stewart are not given. Current excellent data on determining the age of skeletal material by means of the pubic symphysis are not discussed at all. Missing, too, is a discussion of the use of the X-ray in the realm of cephalo-facio-dental growth.

Brožek's chapter is a good summary of his work, which has already been presented in other published media. He makes an important contribution to methodology: skinfolds; limb diameters (muscle and bone); height-weight and their prediction in terms of each other and other skeletal or muscular variables; soft-tissue roentgenography, densitometry, hydrometry; and calculation of total body fat. The data derived from these techniques are applied to problems of body-build, age changes and sex differences, and nutrition in terms of caloric intake and weight (fat).

One might refer to this book in an undergraduate survey course in anthropology. It is not for use at any other (higher) level.

WILTON MARION KROGMAN

CONTRIBUTIONS TO THE PHYSICAL ANTHROPOLOGY OF THE SOVIET UNION. *Russian Translation Series. Peabody Museum Archaeol. Ethnol., Harvard Univ., Vol. 1, No. 2.*

By V. V. Bunak, G. F. Debets, M. G. Levin, and 8 other contributors. Peabody Museum, Cambridge. $4.50 (paper). viii + 192 pp.; ill. 1960.

This volume is supplementary to three publications by Henry Field (*Peabody Museum Papers* 48 (1): 1–154, 1953; University of Miami Press, Coral Gables, Florida, 1956, especially pp. 74–79; *Smithsonian Misc. Collection* 110 (13): 1–244, 1948). Here are 14 papers: A. General anthropological studies: I. Anthropological composition of the population of the Caucasus (V. V. Bunak); III. Preliminary data on the anthropological investigations of the Georgian people (A. N. Natishvili and M. G. Abdushelishvili); IV. Contributions to the anthropology of the Georgian people (A. N. Natishvili and M. G. Abdushelishvili); VI. Anthropological investigations in Daghestan (G. F. Debets); VII. Some material on the anthropology of Daghestan (N. N. Miklashevskaia); VIII. Anthropology of the Avars (M. S. Akimova and M. A. Bulatova); IX. Anthropological type of the Lezghians (M. S. Akimova); XIII. South Siberian anthropological type (M. G. Levin); XIV. Ethnic composition of the Countries of Southwestern Asia (S. I. Bruk); B. Paleoanthropology and archaeology: V. Contribution to the paleoanthropology of the Samthavro Graves (M. G. Abdushelishvili); X. The Eastern Kazakhstan Expedition, 1952 (S. S. Chernikov); XII. Paleoanthropology of the forest tribes of the Northern Altai (V. P. Alekseev) (see II also); C. Craniological studies: II. Craniology of the Caucasus (M. G. Abdushelishvili) (see XII also); D. Methodological studies: XI. Method and program of study of descriptive characters in anthropology and the necessity for their revision (V. V. Bunak).

The foregoing articles include measurements, descriptive traits, blood groups (ABO mainly, with *pqr*), dermatoglyphics, and PTC taste reaction.

It is not possible to do more in this review than to suggest that, as may be expected, the Caucasus area is the focus of Russian anthropological study: linguistically, archeo-culturally, and bioanthropologically. An ancient and basic ethnic foundation is recognized, today most strongly seen in the west-central-north Caucasus. It survives in the Adighe language and in the Pontic race. An ancient but later layer is seen in the eastern Transcaucasus. There are no linguistic survivors, but the south-eastern Caspian race persists, especially in the Tats and the Azerbadzhanis. In the Bronze Age (?) a pre-Georgian culture arose in the western Caucasus, which penetrated to the north. From eastern Anatolia (Van and Zagros areas) there occurred migration of elements to the east Transcaucasus where they are now firmly entrenched.

Russian physical anthropology still places a lot of confidence in traditional "racial" traits, such as the cephalic index and in the reliability of means and their standard deviations as significant criteria of difference. Variance is not considered. Bunak, apparently recognizing the need for tightening up, calls for greater use of photography and the extension of descriptive categories.

WILTON MARION KROGMAN

NATIVE PEOPLES OF SOUTH AMERICA.

By Julian H. Steward and Louis C. Faron. McGraw-Hill Book Company, New York, Toronto, and London. $11.50. xii + 481 pp.; ill. 1959.

In 1946–1950 the Bureau of American Ethnology, Smithsonian Institution, published a 6-volume *Handbook of South American Indians*, under the editorship of Julian H. Steward (*Q. R. B.*, 22: 379. 1947). He and the coauthor, the latter a close associate, and a scholar in the field of South American ethnology, have utilized these materials, and publications

which have appeared since the *Handbook* was prepared. The present work is not a summary or a digest of these materials, but a new and illuminating presentation of the entire field. It deals with problems of presumed or probable relations between the South American continent and Oceania, Middle America, and North America. The principal known culture developments are outlined, from earliest prehistoric times to the days of Spanish conquest and rule, and the contemporary native scene is briefly depicted. The main regional developments in this time span are described. The drama includes the relations of region to region, of culture trait to other traits, of economic and social life to the physiographic setting. This is done with an economy and over-all synthesis not possible in the *Handbook*. Perhaps no other two people could have accomplished this huge task so thoroughly and so deftly. For every interpretation supporting evidence is given. There are several maps, mainly indicating culture areas and the distribution of traits; and there are numerous photographic illustrations. Well-read indeed is he who is not informed and entertained by this panorama of native achievements on a too little known continent. Where else, for example, will one find a people among whom when a man marries a widow he must at the same time marry her daughter?

WILSON D. WALLIS

LEADERSHIP AND CULTURAL CHANGE IN PALAU. *Fieldiana, Anthrop., Vol. 50.*

By Roland W. Force. Chicago Natural History Museum, Chicago. $5.00 (paper). 211 pp.; ill. 1960.

Palau, an island in the west Carolines, Micronesia, is a made-to-order laboratory for the study of culture change. In a period of 50 years it passed from the control of Spain to Germany, to Japan, and in 1944 to the United States. Except in the field of missions, Spain did not interfere a great deal with native life. Germany and Japan did, the latter especially. The Americans, who now administer affairs, attempt to guide the people in the ways of Western democracy and its economy. This involves conflicts of loyalty when choice must be made between adherence to traditionally sanctioned ways and those of the new rulers and their culture.

As in most comparable regions of the world, the young are more favorably disposed toward these efforts than are the elders; and respect for elders is a deep-rooted tradition.

There is a history of changes in the culture and in the framework of social life from days of earliest records to the present. The treatment of so-called leadership spreads a wide net. As used in this study, it includes all native types of superordination, domination, and authority, from high chief to policeman. Some of the "leaders" have no followers; although perhaps most of them do at some time lead some one: the policeman escorts laggards to the jail. Leaders, in the sense in which the term elsewhere is commonly employed, are most successful when they combine outward show of respect for elders and for native traditions with understanding of the purposes of the programs of the present regime.

WILSON D. WALLIS

ADAM'S ANCESTORS. *The Evolution of Man and His Culture. Fourth Edition.*

By L. S. B. Leakey. Harper Torchbooks, Harper & Brothers, New York. $1.60 (paper). xxii + 235 pp. + 22 pl.; text ill. 1960. (Reprint of fourth (1953) edition. New 8 page prologue.)

BIOMETRY

LA BIOMÉTRIE.

By Eugène Schreider. Presses Universitaires de France, Paris. 2 NF. (paper). 128 pp.; ill. 1960.

This book is not a "recipe book" of biometrical formulae, nor is it a discussion of the theory of statistics as applied to biological phenomena. Rather, it is an attempt to justify the application of probability theory to biological observations.

After a short introduction to the use of histograms and the calculation of statistical parameters such as the mean and the standard deviation, Schreider discusses biological measurements. He stresses the variability of measurements from individual to individual, and within the individual from time to time. Such variation, he says, is often due to chance, or to causes which we cannot discern, so that we must impute it to chance. Relationships between measurements, then, cannot be fixed and functional, but must be regarded as variable and probabilistic. He scouts theories based on a viewpoint of absolute functional determinism. He then goes on to discuss the implications of the probability viewpoint in practical problems.

To those of us who, in biological research, are accustomed to this point of view, Schreider's arguments may seem excessive and labored. But this book is one of the "Que sais-je?" series, a series presenting short introductions to a variety of topics, and intended for a general public. Schreider's book, in this context, seems an adequate explanation of the philosophy, if not of the *modus operandi*, of biometrics.

D. P. DOOLITTLE

MODERN PROBABILITY THEORY AND ITS APPLICATIONS.

By Emanuel Parzen. John Wiley & Sons, New

York and London. $10.75. xvi + 464 pp.; ill. 1960.

This is a comprehensive textbook on the theory of probability, with a great variety of examples of application. From p. 6 on, the author makes it clear that the subject is treated here as part of mathematics (deduction from axioms). The first 6 chapters (sample description space; basic theory; independence and dependence; continuous distributions; mean and variance; normal, Poisson, and other probability laws) constitute an introductory course in the mathematical theory of probability which requires 1 year of college calculus. The last 4 chapters are more advanced. Chapters 7 and 8 deal with random variables and their expectations, while 9 and 10 are devoted to the law of large numbers and central limit theorem in a very rigorous manner.

The more difficult a subject is, the more important the method of presentation or exposition becomes, and that is where the art of teaching or writing counts most. Mathematical elegance usually must wait. Considering the materials covered in this book, the author has really tried and succeeded to a very large extent to expose the subject matter clearly. In many instances, a complete enumeration or tabulation of possible results is given so that the reader can "see" how the appropriate answer is obtained.

The organization of the book has several good features, the most important of which is that the exercises (theoretical and numerical ones are separated) are not put at the ends of long chapters, but at the end of each section. This way, the exercises are naturally graded according to the sequence of development of a subject. In fact, this is the principle by which the programs of teaching machines are written. We learn one thing at a time, and what we learn needs immediate reinforcement (by repetition, exercise, analogy, etc.). Textbook writers should make more use of the psychology of learning. It is not sufficient just to write out the proofs.

The materials of the various chapters are classified according to the nature of the problem and not according to mathematical level. Consequently, there are both elementary and advanced sections in each chapter. Fortunately, many of the sections can be read separately, while others may be omitted without losing the continuity. Pure mathematical techniques which are not a part of the theory of probability are separated from the main text and put into an appendix (pp. 160–166). Teachers and students therefore can make their own selection according to their interest and need.

Many more simple diagrams could have been added to illustrate the various theorems. For instance, Bayes' Theorem (p. 119) can be represented very well by a diagram not different from that of Venn. Some problems are treated fully, while others are condensed into a few paragraphs (e.g., pp. 76, 79). This is not necessarily based on the importance of the problem but because the author wants to avoid duplication with other books.

The sum of a large number of independent, identically distributed random variables with finite mean and variance, standardized to have zero mean and unit variance, is approximately normally distributed. This is the so-called "central limit theorem" of probability theory, a name given by G. Polya in 1920. I agree with Parzen when he suggests that a more apt description would be "the normal convergence theorem" (p. 372).

Misprints are rare. There are, however, two of them in one expression ((3.8), p. 106). Perhaps the most amusing one is the sentence: "If the coins are fair, so that $p = \frac{1}{3}$, ..." (p. 104). There are only a few examples from biology. The problem about the probability of having a second hemophilic son (p. 115) may interest geneticists. The biologist should remember that this book is not primarily addressed to students of biology; it is a formal textbook on the mathematical theory of probability; and as such, it ranks with that of Feller and of Uspensky in excellence.

C. C. Li

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